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Contributions

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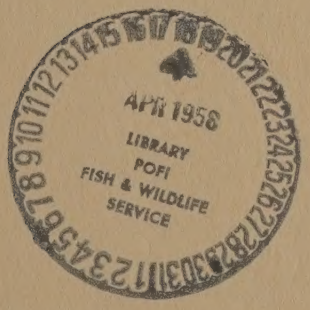
For the Year 1957



THE HAWAII MARINE LABORATORY

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1957 Contributions Available to Date

1 April 1958

[All Contributions published prior to 1 January 1957 have been distributed with the exception of Numbers 44, 49, and 54, Proceedings of the 8th Pacific Science Congress, which are still in press.]

84. Boroughs, Howard, Sidney J. Townsley, and Robert W. Hiatt. 1957. The metabolism of radionuclides by marine organisms. III. The uptake of calcium^{45} in solution by marine fish. Jour. Limnol. and Ocean. 2(1):28-32.

[85. Cushing, John. Serology of tuna. Fishery Bull. of Fish and Wild. Ser. In press.]

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[88. Kohn, Alan. Recent cases of human injury due to venomous marine snails of the genus Conus. Amer. Jour. Trop. Med. and Hygiene. In press.]

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84. Boroughs, Howard, Sidney J. Townsley, and Robert W. Hiatt. 1957. The metabolism of radionuclides by marine organisms. III. The uptake of calcium[45] in solution by marine fish. Limnol. and Oceanog. 2(1):28-32.

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The Metabolism of Radionuclides by Marine Organisms. III. The Uptake of Calcium^{45} in Solution by Marine Fish[1,2]

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Hawaii Marine Laboratory, University of Hawaii

ABSTRACT

To determine whether marine fish required calcium in their diet, or whether they could take up an adequate amount from sea water, non-feeding fish (*Tilapia mossambica*) were put in artificial sea water with calcium^{45}. The uptake was rapid at first, then continued at a slow rate for the duration of the experiment (21 days). The normal concentration ratio of calcium by marine fish is about 20. At 21 days, the ratio of Ca^{45} in the fish to the Ca^{45} in an equal weight of sea water was about 0.6. The readily exchangeable calcium in the fish is therefore only a few per cent of the total. The concentration ratio of 0.6 would seem to preclude the necessity of feeding captive marine fish calcium in order to have an adequate diet. The skeleton contained about 43 per cent of the accumulated Ca^{45}, the integument 24 per cent, the viscera 21 per cent, the gills 8 per cent, and the muscle 4 per cent. The Sr/Ca ratio in marine fish as a whole is about 1:400, but the ratio in normal sea water is about 1:40. This means that marine fish discriminate against strontium either by excreting it faster or by absorbing it less.

During some studies on the metabolism of radiostrontium by marine fishes (Boroughs, Townsley, and Hiatt 1956) it occurred to us that our results may have been influenced to some extent by feeding captive fish an artificial diet which may have been deficient in both calcium and strontium. Although marine fish live in an environment rich in both calcium and strontium, no published information could be found concerning the availability of these elements to fishes directly from the sea water. Because freshwater fishes, such as brook trout and guppies, can accumulate calcium directly from their environment (Lovelace and Podoliak 1952, Rosenthal 1956), we designed a simple experiment to test the hypothesis that marine fish can take up and accumulate calcium from sea water.

MATERIALS AND METHODS

Artificial sea water was made up according to Lyman and Fleming (1940). The total calcium was adjusted so that the low specific activity Ca^{45} which was obtained from Oak Ridge plus the added calcium were just equal to the calcium of sea water. *Tilapia mossambica*, the fish used for these experiments, were kept in carboys containing 946 microcuries of Ca^{45} in 20 liters of water. The water temperature was about 22°C throughout the experiment. The extremes were 20.5° and 23.2°C. The water was aerated, but the fish were not fed during the entire experiment. Six fish were kept in each carboy and three fish were removed at each time interval from four hours to 21 days. The fish were then dissected, ashed, and counted according to the procedure described elsewhere (Boroughs, Townsley, and Hiatt 1956). An aliquot of the dose was counted to correct for decay, and appropriate corrections were made for self-absorption.

RESULTS AND DISCUSSION

Figure 1 shows that *Tilapia*, a sluggish fish, took up the calcium from solution rather rapidly, and that the uptake continued throughout the duration of the experiment. Although the three fish in the three-day carboy were very small in comparison with the other fish used (average weight: 72 g, while the average of all the fish was 102 g), size alone cannot account for the dip in the curve. The same data were plotted in Figure 2 in order to allow for the weight of each

[1] This work was carried out by means of Contract No. AT(04-3)-56 between the U. S. Atomic Energy Commission and the University of Hawaii.
[2] Contribution No. 84, Hawaii Marine Laboratory, University of Hawaii.

fish, and the dip still occurs. A measurement of the radioactivity present in the carboy at the beginning of the experiment showed that this carboy received about 20 per cent less Ca^{45} than did the other carboys. At any rate, we attribute no biological significance to the dip at three days.

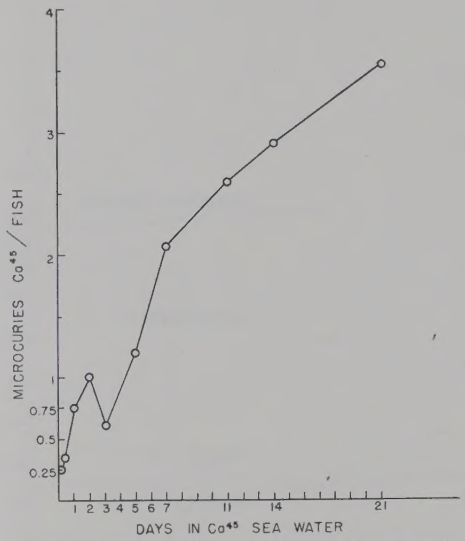

FIG. 1. The rate of uptake of calcium[45] from solution by *Tilapia mossambica*.

Figure 2 also indicates that the concentration ratio achieved during the 21 days is about 0.6. The concentration ratio is here defined as the microcuries/g fresh weight of fish divided by the microcuries/g of sea water. In other words, the internal concentration of calcium had not reached the external concentration.

Figure 3 shows amounts of Ca^{45} recovered in five different organ-systems of *Tilapia*. As one would expect, most of the radioactivity appeared in the skeleton. At 21 days, 43 per cent of the Ca^{45} was in the skeleton, 24 per cent in the integument, 21 per cent in the viscera, 8 per cent in the gills, and 4 per cent in the muscle. This distribution does not correspond to the distribution of non-radioactive calcium in these tissues. On the basis of an elemental analysis of tuna fish by Goldberg (unpublished), and an analysis of the percentage of the total ash contributed by each organ of tuna fish made in this laboratory (Boroughs, Townsley, and Hiatt 1956) it is apparent that about 70 per

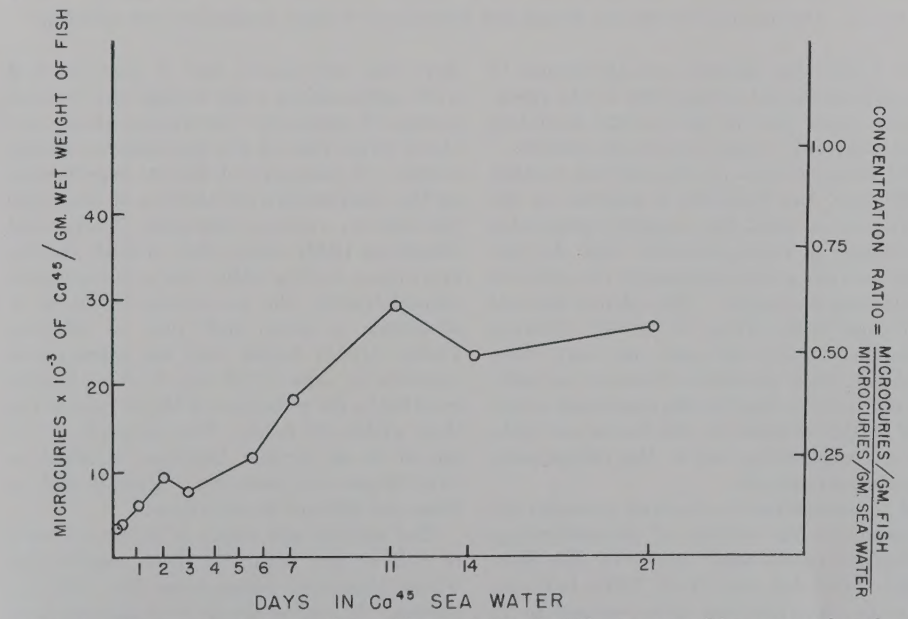

FIG. 2. The rate of uptake of calcium[45] from solution by *Tilapia mossambica* expressed as the concentration ratio.

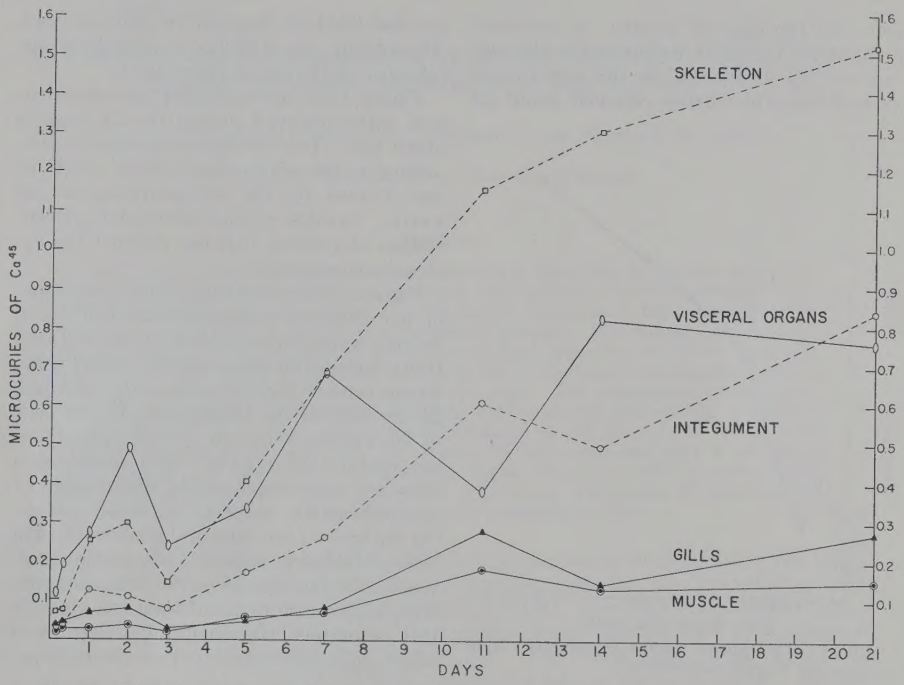

FIG. 3. The internal distribution of calcium^{45} taken up by *Tilapia mossambica* from solution.

cent of the total calcium is in the bones, 15 per cent in the gills, 6 per cent in the integument, 3 per cent in the viscera, including the blood, and 1–2 per cent in the muscle.

We have no data on the calcium content of *Tilapia*, but Goldberg's analysis of the anchoveta, a small fish roughly comparable to *Tilapia* in form, indicates that the calcium content is approximately the same in anchovetas and tuna. The calcium content of *Tilapia* is not likely to be very different from these other fish, and one may infer, therefore, that continued exposure to radiocalcium would result in the continued accretion of this element in the bones and gills, but a comparative loss in the integument, viscera, and muscles.

It is interesting to note that a similar experiment on the uptake of radiostrontium in solution by the same species of fish (Boroughs, Townsley, and Hiatt 1956) indicates that the concentration ratio reached in 21 days was only about half of that reached with radiocalcium even though the concentration of radioactive strontium atoms was about twice that of the radioactive calcium atoms. A summary of several experiments on the comparative metabolism of these two elements in various mammals (Norris and Kisieleski 1948) shows that in both the rat and mouse, and by either oral or intravenous administration, the percentage retention of strontium is about half that of calcium. Pecher (1941) found that the intravenous injection in mice of 0.8 mg of Ca as lactate resulted in the retention of 58 per cent of the dose within 24 hours. The injection of 1.6 mg of Sr as lactate, however, resulted in only 33 per cent retention. Results such as these are difficult to understand.

The authors are aware of no Sr/Ca ratio of 1:2 in any organ of those marine fish whose elemental composition has been reported. If both elements were accumulated

on an equimolar basis, the percentage of strontium in the ash of the organ or organism would be about twice that of calcium, because this is approximately the ratio of their atomic weights. One finds, on the contrary, that the ratio of strontium to calcium is marine fish is of the order 1:400 or less. This means that for each mole of Sr there are approximately 800 moles of Ca. If these same ratios of Sr/Ca obtain in mammals, one might be tempted to ascribe the 1:2 ratio actually found for radiostrontium and radiocalcium to a transient state. In the mammal it is conceivable that a surge of strontium not ordinarily present in the diet might give rise to very high transient ratios. In marine fish, however, such a situation would not be possible unless the fish were dosed with strontium far in excess of the concentrations used in our experiments. These concentrations were in each instance below the concentration of strontium in sea water. The Sr/Ca ratio in sea water is about 1:40 or 5:200. This means that fish discriminate against strontium, in comparison with calcium, either by excreting it faster, or by absorbing it less. The same discrimination against strontium occurs in other animals and in plants as well (Libby 1956; MacDonald, Noyes, and Lorick 1956). This discrimination, coupled with the large concentration of calcium and the relatively large concentration of strontium in sea water, is a fortunate combination which reduces the radiation hazard of this important fission product to some marine organisms and to man as well.

According to various analyses of the calcium content of marine fishes (Vinogradov 1953) there is approximately 20 times as much calcium in a whole fish as there is in an equal weight of sea water. The concentration ratio is therefore 20. This amount of course is quite variable, and depends for the most part upon the age and species of fish. Assuming a concentration ratio of between 0.5 and 0.7 for the 21 day fish, it is evident that only 2–3 per cent of the total calcium in the body is readily exchangeable under the conditions of the experiment. In general, it is considered that the turnover time for bone calcium is very long. Once the calcium is incorporated into some sort of matrix, only a small amount is involved in metabolism under normal conditions, and most of it remains *in situ* for the duration of the animal's life.

The rapid uptake of both calcium and strontium by marine fish, the continuous uptake over at least a 21-day period, and the noteworthy concentration ratio for strontium and calcium of about 1:2 indicate strongly that the artificial diet fed captive tuna during experiments on the uptake, accumulation, and loss of radiostrontium would have had little effect or no effect on the results of the experiments.

SUMMARY

Tilapia mossambica, sluggish marine or brackish water fish, were put in artificial sea water with calcium^{45} so that the total calcium concentration was equal to that of sea water. The fish were not fed during the experiment which lasted 21 days. During this time, the fish as a whole took up the Ca^{45} to the extent of about 60 per cent of the Ca^{45} concentration in the water. Most of the radioactivity was recovered in the skeleton and integument, but the values obtained do not correspond to the elemental analysis of various fish for calcium. Only a few per cent of the body calcium is apparently readily exchangeable. It is concluded that marine fishes can take up calcium directly from sea water, and do not need a dietary source for this element. In comparison with a similar experiment using radiostrontium, it is further concluded that marine fishes discriminate against strontium in favor of calcium.

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NOTES

Sexual Dimorphism in the Labrid Fish Genus *Gomphosus*[1]

During an examination of the viscera of Marshallese fishes the writers' attention was drawn to the fact that all of our specimens of *Gomphosus varius* in which the sex could be determined were females, and that all specimens of *G. tricolor* were males. Suspecting the possibility of sexual dimorphism, we collected additional material, so that this study of *Gomphosus* ultimately included 56 specimens from Eniwetok, 4 from Bikini, 3 from Arno (all atolls in the Marshall Islands), and 15 from Oahu and Kauai in the Hawaiian Islands. Seven Marshallese and 3 Hawaiian specimens were *tricolor*, according to various descriptions; 14 Marshallese specimens were the distinctively marked juveniles of *varius*; and the remaining 54 were typical *varius*. Eight of the 10 *tricolor* proved to be males, one was decomposed internally, and another was too immature to be sexed. Sex could not be determined for any of the 14 juvenile *varius*, but 39 of the larger specimens were females in various stages of maturity while 15 were immature and could not be sexed.

The major taxonomic difference between *tricolor* and *varius* is color and color pattern. In life *tricolor* is a rich blue-green with a vertical yellow-green bar across the trunk near the pectoral insertion. Its head and caudal fin tend to be rather more bluish than the rest of the body, and in large specimens the caudal fin is somewhat lunate. *G. varius* is somberly colored in comparison, being plain black posteriorly and creamy white to light brown anteriorly, each antero-dorsal scale having a dark spot at its base. The breast and cheeks are white or cream, the snout tip is reddish, and a narrow black stripe runs the length of the head at the level of the pupil. Small juveniles of *varius* are bright yellow-green dorsally, plain white laterally and ventrally, and have a pair of lengthwise black stripes from the snout tip to the caudal base. They also differ from larger specimens in that they either lack or are just developing the elongate snout characteristic of the genus. Jordan and Evermann (1905. *U. S. Fish Comm., Bul.* 23: pl. 36) present a color plate of *tricolor* and in the same work (*op. cit.*, p. 289, fig. 125) a black and white drawing of *varius*.

In size, our *tricolor* range from 104 to 166 mm. in standard length, whereas typical *varius* range from 38 to 134 mm. From about 30 to 40 mm. the *varius* and juvenile color patterns intergrade, our largest true juvenile measuring 36 mm. and the smallest 23 mm. Similarly, but on the other end of the scale, our smaller *tricolor* show unmistakable vestiges of a *varius* color pattern, the persistent elements being the basal dark spots on the anterior trunk scales. These spots are more obvious in preserved material than in fresh specimens but some indication of their presence occurs on all *tricolor* examined. The largest *tricolor* have slightly lunate caudal fins, a condition often appearing with age or sex in fishes, and here it is apparently restricted to the male.

Meristic data are the same for the two forms, based on 10 *tricolor* and 19 *varius*. Dorsal rays are VIII, 13; anal rays III, 11 (the first spine is imbedded) although one *tricolor* had only 10 anal rays; pectoral rays are 16, including the short bony splint at the top of the fin, with an occasional specimen having 15 or 17 rays; and lateral line scales are 27. The gill arches are C-shaped and not readily divisible into upper and lower limbs. Gill rakers totalled 24 for the first arch in the two *varius* and two *tricolor* examined for this feature.

The above facts point to the hypothesis that in the Hawaiian and Marshall Islands, at least, the species of *Gomphosus* hitherto regarded as *tricolor* and *varius* are in reality the two sexes of the same species. Apparently *tricolor* represents mature and nearly mature males while *varius* includes all females and probably also young males (even though no recognizable males were found with typical *varius* coloration). Mature males are somewhat larger than the largest fe-

[1] This paper is Contribution No. 86, Hawaii Marine Laboratory, in cooperation with the Department of Zoology and Entomology, University of Hawaii. The senior author was a member of the staff of Duke University at the time the work was done. Manuscript received August 7, 1956.

males and also tend to have lunate caudal fins. More than likely an histological examination of the gonads of small "*varius*" would show both sexes displaying the *varius* or juvenile color pattern.

Marked sexual dimorphism, expressed as coloration differences, is not unusual among the labroid fishes. Longley (Longley and Hildebrand, 1941. Papers from Tortugas Lab. 34: 196–198) showed that in *Thalassoma bifasciatum* only adult males attain the *bifasciatum* color pattern, whereas females and young males exhibit a coloration so characteristic that they were long called *T. nitidum*. Recently Randall (1955. *Copeia* 3: 237) has demonstrated that *Stethojulis renardi* is merely the adult male of *S. strigiventer*, and Brock and Yamaguchi (1954. *Copeia* 2: 154–155) have shown that *Scarus ahula* is the female of *S. perspicillatus*. The latter authors contrast the bright blue, green, and yellow pattern of male *perspicillatus* with the rather drab pattern of the female, a situation quite similar to that obtaining in *Gomphosus*.

One line of evidence which seems to cast doubt on our hypothesis that *tricolor* and *varius* are dimorphic forms of the same species is their pattern of distribution and relative abundance. In the 2-to 35-foot depth range sampled for this study *tricolor* occurred mostly in deeper water and was uncommon even there. *G. varius*, on the other hand, seemed to be uniformly distributed throughout this range and was common to abundant. Every rotenone or sight-observation station yielding *tricolor* also produced *varius*, but the reverse was certainly not true. Disjunctive distributions and aberrant sex ratios such as those found in this study do not necessarily indicate that *varius* and *tricolor* are separate species, particularly in view of Gosline and Strasburg's recent work (1956. *Copeia* 1: 9–18), on the even more markedly dimorphic Hawaiian moringuid eels.

The name to be applied to our *Gomphosus* cannot be verified at this time. *Gomphosus varius* Lacepede (1802. *Hist. Nat. Poiss.* 3:100, 104) predates *G. tricolor* Quoy and Gaimard (1824. Voyage *Uranie*, Zool.: 280), the type localities being Tahiti and the Hawaiian Islands respectively. We accordingly refer our material to *varius*, but with the following reservation. In the Indian Ocean the central Pacific forms of *Gomphosus* are replaced by two or three other species, one or two of which may be identical with the Pacific *varius*. Based on our experience it would appear that sexual dimorphism is also present in the Indian Ocean *Gomphosus*, and that males may occur as either the blue-green *tricolor* form or as a violet-blue species called *coeruleus*. The precise relationship of the Indian Ocean to the Pacific *Gomphosus* remains to be demonstrated. When this is done it may be that what we here call *varius* will be synonymized with *coeruleus*.

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An Annotated List of Marine Algae from Eniwetok Atoll, Marshall Islands[1]

E. YALE DAWSON[2]

Reprinted from PACIFIC SCIENCE
January, 1957

An Annotated List of Marine Algae from Eniwetok Atoll, Marshall Islands[1]

E. Yale Dawson[2]

The following account is based largely upon collections made by the writer at Eniwetok during the late summer of 1955 and upon collections made on several occasions prior to that time by Dr. Ralph F. Palumbo of the Applied Fisheries Laboratory, University of Washington. The object of the work has been the preparation of a reference collection of algae of the atoll for deposition at the Eniwetok Marine Biological Laboratory (EMBL), where it may be consulted by future biological investigators interested in identifying algal research materials.

There exist only three previous accounts of Eniwetok marine algae, namely, Taylor's *Plants of Bikini* . . . (1950) which treats of 67 species, Palumbo's (1950) brief listing of a few entities, most identified only to genus, and Odum and Odum's (1955) mention of four species by name. The most comprehensive list of Marshall Islands algae to date has just been published by the writer (1956) in *Pacific Science*. It treats of 149 species (exclusive of Myxophyta) for the southern Marshall Islands. All but 43 of these are again listed in the present account, which includes 228 species and varieties. Of these, 36 are Myxophyta, 79 Chlorophyta, 20 Phaeophyta, and 91 Rhodophyta.

Inasmuch as this paper can be of greatest service as an aid to the identification of the algae occurring at Eniwetok, a key to all of the genera is included as well as an illustration for each species of Green, Brown, and Red Algae for which a figure is not to be found among the following accounts of tropical Pacific marine algae: Taylor, 1950; Dawson, 1954; Dawson, 1956. If these three papers are employed in conjunction with the present list, one should find it relatively easy to identify a great majority of the species encountered.

It should be noted that the key to the genera is intended to apply specifically to those algae recorded here from Eniwetok Atoll. It does not necessarily apply to species of those genera from other regions.

The short glossary of certain special phycological terms is intended to aid those of other disciplines in the use of the key.

ACKNOWLEDGMENTS

Nearly all of the algal collections cited here other than the writer's were made by Dr. Ralph F. Palumbo, who kindly contributed much time in preparing them for study in Honolulu. The list is considerably more comprehensive as the result of the availability of his specimens, which provide an excellent supplement to mine.

Dr. Francis Drouet provided identifications for all of the Blue-green Algae, so that this

[1] Contribution No. 87 from the Hawaii Marine Laboratory. Manuscript received January 17, 1956.

[2] Associate Biologist (temporary), University of Hawaii; 18328 Plummer Street, Northridge, California.

part of the list may be considered entirely his own contribution.

Dr. Harold St. John kindly prepared the Latin diagnoses of new taxa.

Special thanks are due to Dr. Robert W. Hiatt for making all the arrangements for carrying out this study, and to Dr. Maxwell S. Doty for the use of his library and other facilities in Honolulu. Several others contributed help in various ways, especially Mr. Malvern Gilmartin, Mr. A. Dexter Hinckley, Mr. Robert T. B. Iversen, Mr. James Stewart, Dr. Donald W. Strasburg, and Dr. A. J. Bernatowicz.

Photographs are by Mr. George Edelman.

COLLECTING LOCALITIES

Inasmuch as a number of variations occur in the spelling and application of the names of islands in Eniwetok Atoll, a list is presented here to show the equivalents. The list follows the succession of islands in a clockwise manner, beginning with Bogallua in the northwest part of the Atoll. The first name given in each case is that used in the text and in the labeling of specimens, followed by some common variations which may be encountered on United States maps and in geographical publications.

Bogallua
Bogombogo
Eneroul = Eybbiye = Ruchi (often treated as a single island with the next)
Runo = Eybbiye = Ruchi = Cochiti
Bokanjoio = Sanildefenso
Elugelab
Lidilibut = Teiteiripucchi
Bogairik = Bogeirik
Bokaniuar
Bogon
Engebi
Muzin = Mujinkarikku
Kirinian = Biilee
Bokonaarappu
Yeiri
Aitsu
Rujoru = Lujor = Pujiyoru = Rujiyoru
Eberiru
Aomon = Aranit
Biijiri = Biiziri
Rojoa
Aaraanbiru = Arambiru
Piiraai
Runit
Enedrol
Chinieero
Aniyaanii = Japtan
Chinimi
Japtan = Muti
Bogen = Boken = Jieroru
Parry
Eniwetok
Igurin
Mui = Buganegan
Pokon = Bogan
Ribaion = Libiron = Ribairon
Giriinien = Grinem
Rigili

The following is a complete list of the writer's collections made during August and September 1955. The inclusive field collection numbers precede the locality data in each case. It should be noted that where these numbers are cited in the text they are prefixed by "D." Collection numbers by Palumbo are prefixed by "P.," and, because of their smaller number and scattering in time and space, are provided with locality data in the text. Those collections by Taylor which represent species not again collected are cited by his field number prefixed by "T."

A specimen of each of the Dawson and Palumbo collections cited here is deposited in the Eniwetok Marine Biological Laboratory, with the exception of the type specimens of new species and varieties, which are deposited in the Bernice P. Bishop Museum in Honolulu.

13607–13654. Parry Island, outer seaward reef opposite EMBL, Aug. 19.

13655–13679. Parry Island, seaward reef flat between EMBL and south end of island, Aug. 20.

13680–13692. Parry Island, seaward reef flat at extreme south end of island, Aug. 21.
13693. Parry Island, drift in front of EMBL, Aug. 21.
13694–13712. Parry Island, among coral heads in the lagoon near south end of island in 6 to 10 feet of water, Aug. 21.
13713–13716. Aniyaanii Island, inshore lagoon near landing, Aug. 22.
13717–13745. Aniyaanii Island, seaward reef just on or inside of coralline ridge, Aug. 22.
13746–13781. Aniyaanii Island, under coral and rocks in tidal washes at north side of island, Aug. 22.
13782–13798. Aniyaanii Island, lagoon side among coral heads in 3 to 8 feet of water, Aug. 22.
13799–13824; 13855–13858a. Engebi Island, ocean side reef, Aug. 23.
13825–13827. Engebi Island, on a boulder in middle of ocean side reef, Aug. 23.
13828. Engebi Island, lagoon side drift, Aug. 23.
13829–13854. Engebi Island, algal mat area on dead coral and sand bottom of lagoon side, Aug. 23.
13859–13874. Igurin Island, seaward reef, Aug. 24.
13875–13877. Igurin Island, at depth of 20 feet off edge of seaward reef, Aug. 24.
13878. Igurin Island, sand flat on sea side, Aug. 24.
13879–13880. Igurin Island, seaward reef drift, Aug. 24.
13881–13885. Igurin Island, lagoon side drift near north end, Aug. 24.
13888–13897. Igurin Island, mid-island lagoon in 3 to 6 feet of water, Aug. 24.
13898–13899. Runit Island, lagoon side bottom at about 8-foot depth, Aug. 25.
13900–13908. Runit Island, scraped from a *Tridacna* shell from 20-foot depth in the lagoon, Aug. 25.
13909–13910. Runit Island, lagoon side drift, Aug. 25.
13911–13916. Runit Island, from vertical sides of pier piles in the lagoon, Aug. 25.
13917–13925. Runit Island, on a floating bumper log fastened to the pier, Aug. 25.
13926–13936; 13940–13946. Runit Island, ocean reef flat, Aug. 25.
13937–13939. Runit Island, in the lagoon in 10 feet of water, Aug. 25.
13947–13954. Parry Island, in the lagoon among coral heads in 10 to 12 feet of water, Aug. 28.
13955–13956. ¾ mile off Aniyaanii Island, on lagoon bottom in 90 feet (drift), Aug. 29.
13957–13961. Parry Island, lagoon beach in 6- to 8-foot depths, Aug. 29.
13962–13970. ½ mile off Aniyaanii Island, around and on a dead coral head in the lagoon at 35- to 65-foot depths, Aug. 30.
13971. Parry Island, off lagoon swimming beach in 10 feet of water, Aug. 30.
13972–13983. Parry Island, in end of pipe and beneath outfall of salt water from generating plant opposite EMBL, Aug. 30.
13984–13995. Japtan Island, reef along passage opposite Parry Island, Aug. 30.
13996–14000. 1½ miles off Aniyaanii Island, lagoon bottom at a depth of 135 feet, Aug. 31.
14001–14020. Rigili Island, seaward reef near edge at north end of island, Sept. 2.
14021–14032. Rigili Island, sand bottom in lagoon in 3 to 6 feet of water, Sept. 2.
14033–14039. Rigili Island, at small island on lagoon side subject to prevailing winds, Sept. 2.
14040–14041. Rigili Island, seaward reef, Sept. 2.
14042–14043. Parry Island, lagoon swimming area, Sept. 3.
14044–14053. Parry Island, on and around tanker wreckage adjacent to passage, Sept. 3.

GLOSSARY

chromatophore: a pigment-bearing structure within the cell.
corticated: provided with a complete or incomplete layer of superficial cells over the primary axis of the thallus.

distichous: disposed in two vertical rows; two ranked.
endophytic: growing within another plant.
epiphytic: growing on another plant.
heterocysts: cells which are uniformly dissimilar in shape and (or) size from their neighbors.
intercalary: inserted between, as opposed to terminal or basal.
medulla: the central or inner tissue of a thallus as opposed to the cortex.
midrib: a vein-like or rib-like thickened axis of a blade.
monosporangium: an asexual reproductive organ in the red algae which produces a single spore.
multifarious: disposed in many ranks about an axis.
multiseriate: of more than a single row of cells.
rhizoidal filaments: thick-walled, very long cells of exceedingly small diameter running vertically between the larger cortical cells as in *Gelidium*.
rhizoids: small root-hair-like unicellular or multicellular outgrowths for attachment.
saxicolous: growing on rocks.
stichidium: a club-shaped reproductive branch in the red algae producing tetrasporangia.
tetrasporangium: an asexual reproductive organ in the red algae which produces spores in groups of four.
trabeculae: bars or strands running from one side of a coenocytic thallus to the other, as in *Caulerpa*.
trichoblast: a branched, colorless, hair-like outgrowth produced around the apex of certain red algae, usually soon falling away.
trichome: the individual cellular filament of a multicellular blue-green alga, not including the sheath.
tristichous: disposed in three vertical rows; three ranked.
uniseriate: of a single row of cells.
utricles: the enlarged, bladder-like ends of the filaments of *Codium* which are arranged to make up the surface layer of the thallus.

KEY TO THE GENERA OF MARINE ALGAE OF ENIWETOK

1. Plants unicellular, or apparently so, macroscopic or microscopic, spheroidal, ellipsoidal or club-shaped 2
1. Plants multicellular, or, if noncellular the thalli macroscopic and not solid spheroidal, ellipsoidal or club-shaped . 8
2. Plants microscopic, less than 40 μ in diameter, in pairs or colonies within a gelatinous matrix or sheath, sometimes (in *Entophysalis*) arranged in short filaments 3
2. Plants macroscopic, bladder-like 7
3. Colonies showing no particular orientation into basal and apical regions 4
3. Colonies showing orientation of cells into basal and apical regions . . . . . **Entophysalis (deusta)**
4. Colonies without definite shape; cells symmetrically ellipsoidal 5
4. Colonies with a definite shape; cells pear-shaped . . . . . **Gomphosphaeria**
5. Cells spheroidal, or hemispheroidal when divided 6
5. Cells elongate ellipsoidal . . . . . **Coccochloris**
6. Cells usually single or paired, enclosed in a thick, gelatinous sheath . **Anacystis**
6. Cells forming colonies within a gelatinous matrix . . **Entophysalis (conferta)**
7. Thalli spheroidal, attached by small unbranched rhizoids cut off by a septum from the main cell . . . . . **Valonia (ventricosa)**
7. Thalli short club-shaped, attached by branched, nonseptate rhizoids . . . . . **Boergesenia**
8. Thalli multicellular or noncellular, branched if uniseriate 9
8. Thalli multicellular, but each filament consisting of only an unbranched row of cells (the false branching in *Plectonema* and *Scytonema* is the result of protrusion of a broken trichome through a rupture in the sheath) 99

9. Thalli not minute borers through calcareous material 10
9. Thalli boring through coral, shell and other calcareous material . . **Ostreobium**
10. Thalli calcified, either completely so as to become hard and stony, or incompletely so as to appear limy 11
10. Thalli not calcified 24
11. Thalli essentially prostrate, crustose; if erect branches present, these inflexible and stony 20
11. Thalli erect and flexible, not prostrate or crustose 12
12. Thalli not parasol-shaped 13
12. Thalli shaped like a small parasol . . . . . **Acetabularia**
13. Thallus parts of cylindrical shape . . . 14
13. Thallus parts flat or flattened 18
14. Thalli branched 15
14. Thalli unbranched (as viewed macroscopically) . . . . . **Neomeris**
15. Thalli distinctly jointed 17
15. Thalli not distinctly jointed 16
16. Thalli soft and lubricous . . . . . **Liagora**
16. Thalli firm, not lubricous . . . **Galaxaura**
17. Thalli large and coarse, the segments 2 to several mm. in diameter . . . . . **Halimeda (monile** forms)
17. Thalli small and delicate, the segments less than ½ mm. in diameter . . . . **Jania**
18. Thalli not jointed, fan-shaped 19
18. Thalli jointed . . . . . **Halimeda** (except **monile** forms)
19. Thalli brownish, with prominent concentric banding . . . . . **Padina**
19. Thalli greenish, not prominently banded concentrically . . . . . **Udotea**
20. Thalli forming thin, adherent crusts . 21
20. Thalli forming massive, stony crusts, sometimes with erect knobs or branches . . . . . **Porolithon**
21. Thalli epiphytic, very delicate 22
21. Thalli saxicolous, coarser 23
22. Thalli in surface view with frequent larger cells (heterocysts) among the otherwise uniform cells . . . . . **Fosliella**
22. Thalli in surface view composed of uniform cells . . . . . **Heteroderma**
23. Underside of thallus of many fan-shaped groups of cells converging and diverging irregularly . . . . . **Cruoriella**
23. Underside of thallus of essentially parallel cell rows . . . . . **Peyssonelia**
24. Thalli filamentous, membranous, or massive, but in any case divided up into cells by cross walls 31
24. Thallus parts not divided up in a cellular manner by cross walls 25
25. Filaments composing thalli dichotomously branched 26
25. Thalli, or filaments composing thalli, not dichtomously branched 29
26. Filaments growing together to form a flabellate or peltate, spongy plant body 27
26. Filaments free, not forming a spongy plant body 28
27. Main forked filaments bearing numerous terminally pronged lateral branchlets . . . . . **Rhipilia**
27. Main forked filaments without such terminally pronged lateral branchlets . . . . . **Avrainvillea**
28. Filaments over 100 μ in diameter above, tending to be larger above than below, not attenuated . . **Pseudochlorodesmis**
28. Filaments usually under 50 μ in diameter above, attenuated or at least of lesser diameter above than below . . **Derbesia**
29. Thallus parts spongy, composed of interlaced filaments forming a surface layer of swollen utricles . . . . . **Codium**
29. Thallus parts not spongy, without a surface layer of swollen utricles 30
30. Thalli consisting of basal, cylindrical rhizoid-bearing parts and erect, specialized branches of distinctive shapes; interior of thallus criss-crossed by trabeculae . . . . . **Caulerpa**
30. Thalli consisting of erect axes bearing pinnate or multifarious branches; interior without trabeculae . . . . **Bryopsis**

31. Thallus essentially of a single branched row of cells 32
31. Thallus filamentous, membranous or massive, consisting of more than a single, branched row of cells 51
32. Filaments prostrate, spreading; plants microscopic, epiphytic or endophytic . . . . . **Entocladia**
32. Not as above; filaments free and more or less erect 33
33. Individual cells mostly essentially cylindrical and symmetrical except for curvature 35
33. Individual cells asymmetrical, mostly not cylindrical 34
34. Cells protruding irregularly on all sides from the axes . . . . . **Siphonocladus**
34. Cells inflated, irregularly clavate to subovate, in short, more or less repent series of only a few cells . . . . . **Valonia** (in part)
35. Thallus filaments branched in one plane in a fan-, or blade-like manner, at least in part 36
35. Thallus filaments variously branched, but not forming fan- or blade-like parts 38
36. Filaments palmately branched . . . . . **Rhipidiphyllon**
36. Filaments not palmately branched; blades of net-like form 37
37. Blades stalked . . . . . **Struvea**
37. Blades without a definite stalk . . . . . **Microdictyon**
38. Branches essentially free, not attached to each other 39
38. Branches attached to each other by small, specialized cells . . . . . **Boodlea**
39. Branching opposite or whorled, at least on main or lower axes 40
39. Branching alternate or irregular, multifarious 41
40. Axes with whorled branchlets; tetrasporangia surrounded by curved filaments . . . . . **Wrangelia (argus)**
40. Main axes (sometimes prostrate) with opposite and distichous or tristichous branchlets; tetrasporangia not associated with curved filaments . . . . . **Antithamnion**
41. Cell wall about as thick as cell cavity, at least in lower parts 42
41. Cell cavity much greater in diameter than cell wall thickness 43
42. Cell cavities oval, longer than broad . . . . . **Asterocytis**
42. Cell cavities more or less quadrangular, broader than long . . . . . **Goniotrichum**
43. Thalli brownish or reddish, bearing specialized external reproductive structures 46
43. Thalli greenish, without specialized external reproductive structures 44
44. Filaments bearing septa at base of branches 45
44. Filaments mostly, or commonly, without septa at base of branches . . . . . **Cladophoropsis**
45. Filaments coarse, 1–2 mm. in diameter . . . . . **Valonia (fastigiata)**
45. Filaments 0.3–1.0 mm. in diameter . . . . . **Valoniopsis**
45. Filaments delicate, less than 200 μ in diameter . . . . . **Cladophora**
46. Thalli brownish, commonly reproducing by means of multicellular gametangia . . . . . **Ectocarpus**
46. Thalli reddish, commonly reproducing by means of tetrasporangia or monosporangia 47
47. Minute epiphytes with main axes less than 15 μ in diameter 48
47. Epiphytic or saxicolous, but main axes over 70 μ in diameter 49
48. Chromatophores stellate . . . . . **Kylinia**
48. Chromatophores not stellate . . . . . **Acrochaetium**
49. Asexual reproduction by tetrasporangia 50
49. Asexual reproduction by monosporangia . . . . . **Neomonospora**

50. Branching regularly alternate and generally spirally arranged; axes less than 100 μ in diameter.....**Callithamnion**
50. Branching irregular; axes over 100 μ in diameter.....**Griffithsia**
51. Thalli consisting of a subcylindrical axis bearing coarse, angular, toothed lateral branches.....**Turbinaria**
51. Thalli not as above.....52
52. Thallus net-like, at least in part....53
52. Thallus not net-like.....55
53. Thallus reddish, delicate, flat or four-sided.....54
53. Thallus brown, coarse, convoluted.....**Hydroclathrus**
54. Net-like parts formed as part of flabellate blades.....**Hemitrema**
54. Entire thallus a four-sided net-like form around a central axis.....**Dictyurus**
55. Thallus cushion-shaped or subspherical, solid or hollow, with cells of macroscopic size.....**Dictyosphaeria**
55. Thallus not as above; cells not of macroscopic size.....56
56. Thallus hollow-tubular or with hollow, vesicular or tubular parts.....57
56. Thallus without hollow parts.....62
57. Thallus without regular constrictions or cavity partitions.....58
57. Thallus regularly constricted and with partitions across the cavity at the constrictions.....**Champia**
58. Thalli hollow essentially throughout.....59
58. Thalli consisting of a short, solid stipe bearing one or more hollow vesicles.....**Botryocladia**
59. Thallus parts long and slender compared to diameter.....60
59. Thallus parts short and inflated compared to diameter.....**Rosenvingea**
60. Thalli reddish; the tube wall composed of several cell layers.....61
60. Thalli greenish; the tube wall composed of a single layer of cells.....**Enteromorpha**
61. Tetrasporangia borne in swollen, terminal stichidia.....**Coelothrix**
61. Tetrasporangia borne in sunken cavities in the branches.....**Lomentaria**
62. Thalli flat or markedly flattened, at least in part.....63
62. Thalli essentially cylindrical (sometimes moderately compressed as in *Hypnea*).....75
63. Thalli brownish or reddish, not green, of more than one layer of cells, at least at the midrib if present.....64
63. Thalli green, of a single layer of cells throughout.....**Anadyomene**
64. Thallus with a midrib (note that the flattened blade part is very narrow in *Taenioma*).....65
64. Thallus without a midrib.....67
65. Color reddish; branching not at all dichotomous.....66
65. Color brownish; branching subdichotomous.....**Dictyopteris**
66. Apices with two or three terminal hairs.....**Taenioma**
66. Apices with a naked apical cell.....**Hypoglossum**
67. Thallus surface covered with tufts of soft but mostly erect filaments.....**Dasyopsis**
67. Thallus surface without tufts of filaments.....68
68. Thalli prostrate and fastened by the lower surface.....69
68. Thalli essentially erect, free, not prostrate.....71
69. Thalli brown.....70
69. Thalli red.....**Rhodymenia**
70. Thalli fan-shaped.....**Pocockiella**
70. Thalli dichotomously branched.....**Dictyota (patens)**
71. Growing points not in apical pits...72
71. Growing points in apical pits.....**Laurencia (parvipapillata)**
72. Growing point consisting of a single apical cell.....73

72. Growing point without a distinguishable apical cell . . . . . **Grateloupia**
73. Thalli small, narrow, less than 1 cm. tall; medulla of several layers of small cells 74
73. Thalli moderately large, 3–10 cm. tall; medulla of a single layer of large cells . . . . . **Dictyota** (in part)
74. Medulla with rhizoidal filaments running through it . . . . . **Gelidium**
74. Medulla without rhizoidal filaments running through it . . . . . **Gelidiella (bornetii)**
75. Axes and branches all similar in appearance and structure **80**
75. Axes distinct from ultimate branchlets in appearance and structure 76
76. Branchlets produced in whorls . . . . . **Wrangelia** (in part)
76. Branchlets produced alternately or irregularly 77
77. Branchlets not banded 78
77. Branchlets banded . . . . . **Spyridia**
78. Branchlets multiseriate; plants rather large, 6–12 cm. tall . . . . . **Asparagopsis**
78. Branchlets uniseriate; plants small, usually less than 2 cm. tall 79
79. Main axes completely or incompletely corticated . . . . . **Dasya**
79. Main axes uncorticated . . . . . **Heterosiphonia**
80. Thallus parts of essentially uniform cell structure throughout; not banded although sometimes appearing segmented 81
80. Thallus parts provided with discontinuous cortication in the form of bands around a large axial cell row, the bands usually close together above and well separated below . . . . . **Ceramium**
81. Thalli of various reddish and brownish colors, but not grass green 82
81. Thalli grass green in color, entangled . . . . . **Enteromorpha (ralfsii)**
82. Branches provided with whorls of short, tooth-like spines, at least in part . . . . . **Centroceras** (in part)
82. Branches without whorls of spines . . 83
83. Middle and upper thallus parts showing only a few cells (2–5) across the diameter when seen in surface view 84
83. All thallus parts showing many (10 or more) small cells across the diameter when seen in surface view 89
84. Branches termination in a large apical cell of nearly the same diameter as the filament bearing it . . . . . **Sphacelaria**
84. Branches terminating in an apical cell which is much smaller than the diameter of the filament bearing it 85
85. Thalli with definite axes provided with dense, multifarious, divaricately branched short branchlets which in mature plants become attached to each other . . . . . **Tolypiocladia**
85. Branching not as above 86
86. All branches essentially of unlimited growth 87
86. Branches of potentially unlimited growth alternating with groups of branches of definitely limited growth . . . . . **Herposiphonia**
87. Erect filaments arising from extensive prostrate creeping filaments . . . . . **Lophosiphonia**
87. Without extensive prostrate filaments 88
88. Mature filaments composed of cells in tiers of three . . . . . **Falkenbergia**
88. Mature filaments composed of cells in tiers of four or more . . . . **Polysiphonia**
89. Surface cells not arranged in regular rows, nor the thallus appearing segmented 90
89. Surface cells arranged in horizontal and vertical rows and the thallus appearing somewhat segmented . . . . . **Centroceras (apiculatum)**
90. Thallus without a central core of small cells in the medulla 91
90. Thallus in cross section showing a core of very small cells in the center of the medulla . . . . . **Dicranema**

91. Medullary cells all similar and more or less isodiametrical in cross section. . 92
91. Thallus in cross section showing minute rhizoidal filaments between the medullary cells . . . **Gelidium (crinale)**
92. Growing points consisting of an apical cell, either emergent or in an apical pit 95
92. Apices without a single apical cell . . . 93
93. Branching irregular, but not markedly divaricate; thalli very slender and wiry 94
93. Branching markedly divaricate; thalli moderately coarse and succulent . . . . . **Chnoospora**
94. Tetrasporangia and antheridia borne in swollen, terminal stichidia; thalli forming small tufts and clumps; main branches mostly 175–250 μ in diameter . . . . . **Gelidiopsis**
94. Reproduction not to be expected; thalli forming wiry mats; main branches (100) 140–230 μ in diameter . . **Wurdemannia**
95. Apical cell in a terminal pit 96
95. Apical cell emergent 97
96. Thalli erect or with creeping and erect branches, with many very short ultimate branchlets . . . . . **Laurencia** (in part)
96. Thalli creeping, with few very short ultimate branchlets . . . . . **Chondria (repens)**
97. Thalli minute, mostly under 2 mm. high 98
97. Thalli larger, 1–3 cm. high . . . **Hypnea**
98. Growing points without trichoblasts . . . . . **Gelidiella (tenuissima)**
98. Growing points provided with short trichoblasts . . . . . **Chondria** (in part)
99. Individual filaments (trichomes) tapering from base to apex 100
99. Individual filaments not tapered, of approximately equal diameter throughout 101
100. With intercalary heterocysts . **Calothrix**
100. With basal heterocysts . . . . . **Rivularia**
101. Filaments epiphytic, erect, attached by a single, modified basal cell . . . . . **Erythrotrichia**
101. Filaments epiphytic or saxicolous, but entangled and without any evident specialized basal attachment cell on individual filaments 102
102. Filaments with false branching by protrusion of trichomes through breaks in the sheath; heterocysts present or absent 103
102. Individual filaments without false branching 104
103. Heterocysts present . . . . . **Scytonema**
103. Heterocysts not present . . **Plectonema**
104. Heterocysts present . **Hormothamnion**
104. Heterocysts not present 105
105. Without a sheath around the uniseriate filament 106
105. Uniseriate filaments surrounded by a sheath 109
106. Filaments straight or curved, but not spirally coiled 107
106. Filaments spirally coiled . . . . **Spirulina**
107. Cells very short, less than half as long as broad . . . . . **Oscillatoria**
107. Cells not very short, generally longer than broad; filaments generally over 20 μ in diameter 108
108. Filaments 20–30 μ in diameter . . . . . **Rhizoclonium**
108. Filaments 60–90 μ in diameter . . . . . **Chaetomorpha**
109. Cells very short, less than half as long as broad 110
109. Cell length about equal to or greater than breadth 111
110. Sheaths distinct, firm; trichomes single within the sheath . . . . . **Lyngbya**
110. Sheaths more or less mucous, diffluent; trichomes several within the sheath . . . . . **Hydrocoleum**
111. Trichomes single within the sheath 112
111. Trichomes many within the sheath, at least in older parts 115
112. Trichomes 3 μ or less in diameter . . 113

112. Trichomes 5 μ or more in diameter. 114
113. Plant body a light colored, cushion-shaped form . . . . . **Phormidium (crosbyanum)**
113. Plant body a dark colored stratum . . . . . **Symploca (laete-viridis)**
114. Plant body an erect, spongy, brush-like tuft . . . . . **Symploca (muscorum)**
114. Plant body a loose, soft group of short, gelatinous strings . . . . . **Phormidium (penicillatum)**
115. Apical cell blunt-conical . . **Schizothrix**
115. Apical cell acutely conical . . . . . **Microcoleus**

SYSTEMATIC LIST

GREEN ALGAE

Enteromorpha acanthophora Kützing?
D. 13920a. A few small bits of uncertain identity.

Enteromorpha clathrata (Roth) J. Agardh; Dawson 1954: 384, fig. 6d, e; Dawson 1956: 27
D. 13961.

Enteromorpha intestinalis (Linnaeus) Link; Dawson 1954: 383, fig. 6c
D. 13917.

Enteromorpha kylinii Bliding; Dawson 1954: 384, fig. 5; Dawson 1956: 27
D. 13826. P. 2846, Bokanjoio Is. boat passage at 6 ft., 9/30/54.

Enteromorpha ralfsii Harvey; Dawson 1956: 27, fig. 2
D. 13792, 14024. P. 1187, Bokanjoio Is. tide flats, 4/14/54; P. 2849, Bokanjoio Is. seaward tide flats, 9/29/54; P. 18150, Runo Is. tide flat pool, 2/10/55.

Enteromorpha tubulosa (Kützing) Kützing; Dawson 1954: 384, fig. 6a, b
D. 13920.

Valonia aegagropila C. Agardh; Dawson 1954: 388, fig. 8j; Dawson 1956: 28; Taylor 1950:41
D. 13610, 13736, 13930, 14039.

Valonia fastigiata Harvey ex J. Agardh 1887: 101 (Ceylon)
Fig. 1

P. 29x, Mui Is. seaward tide flats under rocks in large clumps, 3/11/54.
This compares well with the species as understood by Egerod (1952) and with Kanda's fig. 9A (1944) of a plant from Koror.

Valonia utricularis (Roth) C. Agardh; Dawson 1956: 28, fig. 3
P. 7, Rigili Is. under rocks, 8/10/49; P. 2836c, Parry Is. seaward reef edge, 4/4/54.

Valonia ventricosa J. Agardh; Dawson 1954: 388, fig. 8e; Dawson 1956: 28
D. 13751, 13927, 14002.

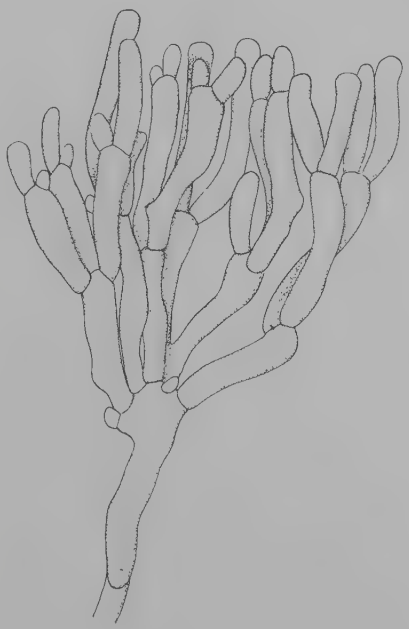


FIG. 1. *Valonia fastigiata*: Habit of part of a plant of P. 29x, × 2.5.

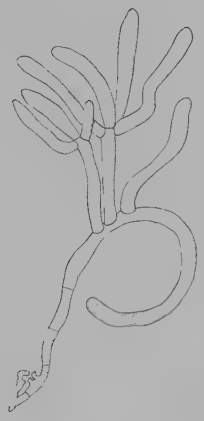


FIG. 2. *Valoniopsis pachynema*: Part of a plant to show branching and septation, × 5 (after Børgesen).

Valoniopsis pachynema (Martens) Børgesen 1934: 10, figs. 1, 2; Taylor 1950: 42. *Bryopsis pachynema* Martens 1866: 24, pl. 4, fig. 2 (Sumatra)

Fig. 2

T. 46–379. Not collected again.

Boergesenia forbesii (Harvey) Feldmann; Dawson 1954: 388, fig. 8d; Taylor 1950: 41 (as *Valonia forbesii* Harv.)
D. 13732.

Dictyosphaeria cavernosa (Forskål) Børgesen; Taylor 1950: 43, pl. 27, fig. 2; Dawson 1954: 388, fig. 8i; Dawson 1956: 29
D. 13758, 14009.

Dictyosphaeria intermedia var. *intermedia* Weber van Bosse 1905: 14; Taylor 1950: 42; Dawson 1956: 29

Fig. 3

D. 13719. P. 2825, Runo Is. seaward reef edge, 3/8/55.

Dictyosphaeria versluysii Weber van Bosse; Dawson 1954: 388, fig. 8k, l; Dawson 1956: 29
D. 13753, 13675. P. 2821, Bokanjoio Is. seaward reef edge, 3/8/55.

Cladophoropsis gracillima Dawson, prox.; Dawson 1956: 30, fig. 7a, b
D. 14049. The material approaches this species closely but does not agree as fully as the specimens reported from Arno Atoll. The filaments are about 40 μ in diameter and have cells 25–50 diameters long.

Cladophoropsis sundanensis Reinbold; Dawson 1956: 30, fig. 8; Dawson, Aleem, and Halstead 1955: 10
D. 13909.

Siphonocladus rigidus Howe; Dawson 1956: 31, fig. 9
D. 13742a, growing in a mat of *Cladophora*.

Boodlea composita (Harvey) Brand; Taylor 1950: 44; Dawson 1954: 390, fig. 9c, d; Dawson 1956: 30
D. 13764, 13777, 13810, 13854, 13873, 13944, 14031. P. 2840, Eneroul Is. seaward tide flats, 9/23/54.

Boodlea siamensis Reinbold 1901: 107 (Thailand); Taylor 1950: 44
T. 46–400. Not collected again.

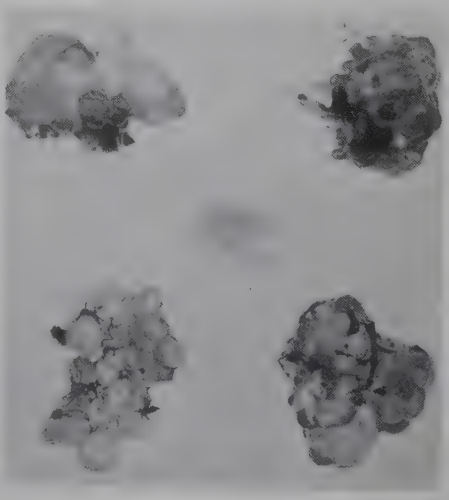


FIG. 3. *Dictyosphaeria intermedia*: Several fresh specimens of D. 13719, × 1.6.

Struvea anastomosans (Harvey) Piccone; Dawson 1954: 390, fig. 8g; Dawson 1956: 30
D. 13650, 13669, 13863, 13989, 14010.

Rhipidiphyllon reticulatum Askenasy; Dawson 1956: 32, fig. 10; Taylor 1950: 45
D. 13778, 14035a.

Microdictyon okamurai Setchell; Taylor 1950: 46, pl. 27, fig. 1; Dawson 1956: 32, fig. 11a
D. 13762, 13945. P. 54–18, Aitsu Is. seaward reef rim, 3/10/54; P. 2844, Bogombogo Is. seaward tide flats, 10/5/54.

Microdictyon japonicum is reported by Palumbo (1950) from Eniwetok without locality, based upon a determination by Lois Eubank Egerod.

Anadyomene wrightii Gray; Dawson 1954: 390, fig. 9e; Dawson 1956: 31
D. 13740.

Chaetomorpha indica Kützing; Dawson 1954: 386, fig. 6f, g; Dawson 1956: 33
D. 13982. P. 2842, Eneroul Is. seaward flats, 9/23/54; P. 2848, Bokanjoio Is. seaward flats, 9/29/54. These are apparently of the same entangled, free form found at Majuro Atoll without holdfast cells.

Rhizoclonium implexum (Dillwyn) Kützing 1845: 206; Smith 1944: 62, pl. 8, fig. 3. *Conferva implexa* Dillwyn 1809: 46, pl. B (England)

Fig. 4*a*

D. 13835, 14049a. This species is treated by Hamel under his genus *Lola*.

Cladophora crystallina (Roth) Kützing; Dawson 1956: 33, fig. 13b, c
D. 13923. The branches in this material range from 85 to 30 μ or less in diameter.

Cladophora inserta Dickie, variations; Dawson 1954: 388, fig. 7d (as *C. inserta* var. *ungulata*)

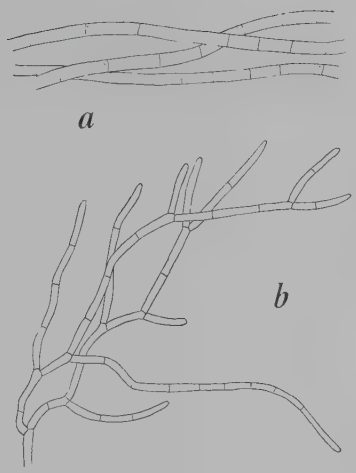


FIG. 4. *a*, *Rhizoclonium implexum*: Parts of filaments, × 80. *b*, *Cladophora socialis:* Part of a plant of D. 13742 near the typical form of the species, × 17.

D. 13837, 13857, 13903b. P. 2813, Bokanjoio Is. lagoon on stake in 3–8 ft., 3/8/55. Some of these specimens apparently correspond with var. *ungulata* (Brand) Setchell.

Cladophora socialis Kützing; Dawson 1956: 34; Dawson 1954: 388, fig. 7e (as *C. patentiramea* var. *longiarticulata* Reinbold)

Fig. 4*b*

D. 13699, 13742, 13806. These specimens seem to represent the same species collected by the writer in Viêt Nam and at Jaluit Atoll in the Marshall Islands. D. 13699 agrees especially well with Børgesen's Mauritius plant called *C. patentiramea* in 1940.

Cladophora luteola Harvey is reported by Palumbo (1950) from Eniwetok based upon a determination by F. Drouet, but a specimen so named by him from Bikini Atoll seems to be *Boodlea*.

Entocladia viridis Reinke; Dawson 1954: 388, fig. 7i
D. 13835a, in the cell wall of *Rhizoclonium*.

Derbesia attenuata Dawson 1954: 390, fig. 9a, b; Dawson 1956: 34
D. 13999b, epiphytic on *Halimeda;* D. 13767a, on small algae.

Derbesia marina (Lyngbye) Solier; Dawson 1956: 34, fig. 15a, b
D. 14006a, epiphytic on *Caulerpa.*

Derbesia ryukiuensis Yamada and Tanaka; Dawson 1956: 34, fig. 14b
D. 13710, 13791.

Bryopsis indica A. and Ethel Gepp; Dawson 1956: 34, fig. 14a; Taylor 1950: 50
D. 13730.

Bryopsis hypnoides Lamouroux 1809: 135, pl. 5, fig. 2 (Mediterranean Sea); Hamel 1931: 394, fig. 20 B; Smith 1944: 73, pl. 9, fig. 2

Fig. 5*a, b*

D. 13977.

Bryopsis pennata Lamouroux; Taylor 1950: 51; Dawson 1954: 393, fig. 11b; Dawson 1956: 34
D. 13703, 13797, 13859, 13907. P. 2855, Bogallua Is. lagoon pavement, 11/17/54. Considerable variation in branching occurs between examples corresponding to the type of the species and those better referred to the following variety.

Bryopsis pennata var. *secunda* (Harvey) Collins and Hervey 1917: 62; Taylor 1950: 52. *Bryopsis plumosa* var. *secunda* Harvey 1858: 31, pl. 45A, figs. 1–3 (Key West, Florida)
P. 52–31, Aomon Is. seaward reef, 10/22/52; P. 52–110, Engebi Is. lagoon, 11/8/52; P. 2585, Aitsu Is. 2/11/55; P. 2851, Bogombogo Is. seaward flats, 10/5/54; P. 2857, Aitsu Is. lagoon, 11/17/54.

Caulerpa acuta (Yamada) Yamada 1944: 34. *Caulerpa filicoides* Yamada 1936: 135, pl. 30, fig. 2. *Caulerpa verticillata* f. *acuta* Yamada 1934: 63, fig. 32 (Naha, Ryukyu Archipelago)

Figs. 6, 7

D. 13875, 13971, 14050.

Caulerpa antoensis Yamada; Dawson 1956: 36, fig. 20; Taylor 1950: 55, pl. 28, fig. 2 (as *C. arenicola* Taylor)
D. 13832.

Caulerpa bikiniensis Taylor 1950: 66, pl. 33 (Bikini Atoll, Marshall Is.)
D. 13774. The material is rather small and incompletely developed, but is apparently identical with Taylor's Bikini and Rogelap specimens. The problem of its relationship and possible varietal status in the *Caulerpa racemosa* complex cannot be taken up here.

Caulerpa brachypus Harvey 1859: 332 (Japan); Taylor 1950: 56, pl. 29, fig. 2
T. 46–422. Not collected again.

FIG. 5. *Bryopsis hypnoides*: *a*, Habit of part of a plant of D. 13977, × 5; *b*, detail of branching of the same, × 45.

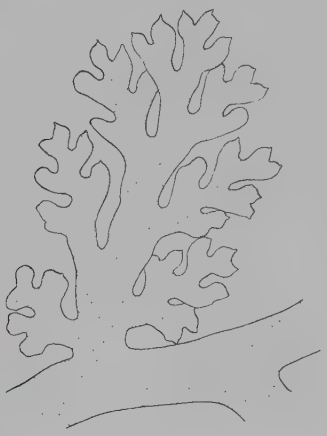


FIG. 6. *Caulerpa acuta*: A small part of a blade of D. 13875 to show ultimate branching, × 100.

Caulerpa elongata f. *disticha* Taylor 1950: 55, pl. 52, fig. 1; Dawson 1956: 37 (as *C. elongata*)

D. 13723. *Caulerpa elongata* is supposed to be distinguished from similar forms of *C. webbiana* by its more lax and erect habit and absence of the abundant ramified filaments from the stolons. However, this specific distinction needs study. Taylor's plant is probably the same as that treated as *C. webbiana* f. *elegans* by Yamada and Tanaka 1938: 62, fig. 4.

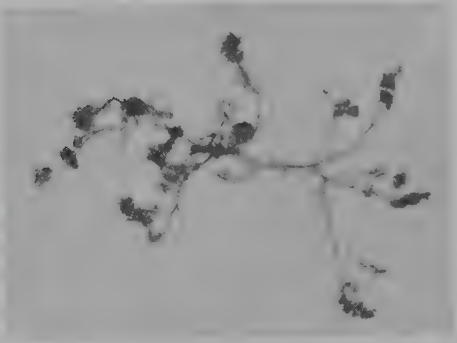


FIG. 7. *Caulerpa acuta*: A dry specimen of D. 13875, × 1.2.

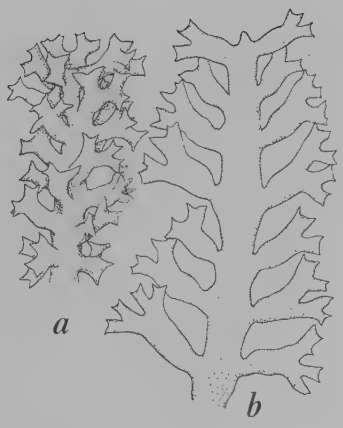


FIG. 8. *a*, *Caulerpa webbiana*: Upper part of a plant of D. 13679, × 22. *b*, *Caulerpa webbiana* f. *disticha*: Upper part of a plant of D. 13892, × 22.

Caulerpa webbiana Montagne 1838: 129, pl. 6 (Canary Islands); Eubank 1946: 415

Fig. 8*a*

D. 13679, 13807. P. 13, Igurin Is. seaward reef, 8/9/49.

Caulerpa webbiana var. *disticha* Weber van Bosse 1898: 270, pl. 21, fig. 1a–c (type locality not indicated)

Fig. 8*b*

D. 13626, 13850, 13864, 13892.

Caulerpa serrulata var. *serrulata* (Forskål) J. Agardh; Taylor 1950: 57, pl. 29, fig. 1, pl. 30, fig. 1; Dawson 1954: 393, fig. 10a; Dawson 1956: 38, fig. 23

D. 13952, 14047. P. 1225B, Parry Is. lagoon in 6 ft., 4/19/54.

Caulerpa racemosa var. *laetevirens* (Montagne) Weber van Bosse 1898: 366, pl. 33, figs. 8, 16–22; Taylor 1950: 64. *Caulerpa laetevirens* Montagne 1845: 16 (Toud Island)

Fig. 9*a*

D. 13628.

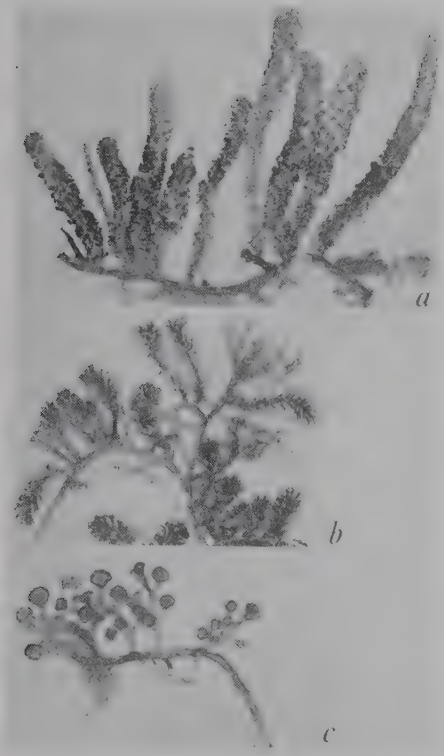


FIG. 9. *a*, *Caulerpa racemosa* var. *laetevirens*: Upper part of a plant of D. 13628, × 0.38. *b*, *C. racemosa* var. *laetevirens* f. *compressa*: Part of a plant of D. 13743, × 0.43. *c*, *C. racemosa* var. *clavifera*: A dry specimen of P. 12, × 0.75.

Caulerpa racemosa var. *laetevirens* f. *compressa* Taylor 1950: 64 (Eniwetok Atoll, Marshall Is.)

Fig. 9*b*

D. 13743, 13812.

Caulerpa racemosa var. *clavifera* (Turner) Weber van Bosse 1898: 361, pl. 33, figs. 1–5; Taylor 1950: 62. *Fucus clavifer* Turner 1808: 126, pl. 57 (Red Sea)

Fig. 9*c*

P. 12, Japtan Is. seaward reef, 8/8/49.

Caulerpa racemosa var. *peltata* (Lamouroux) Eubank; Dawson 1956: 35, fig. 16b; Taylor 1950: 65 (as *Caulerpa peltata* Lamx.)

D. 13735, 13793. The former have peltate foliar ramelli with dentate margins.

Caulerpa racemosa var. *peltata* f. *nummularia* (Harvey ex J. Agardh) comb. nov. *Caulerpa nummularia* J. Agardh 1872: 38 (Friendly Islands,-Tonga) *Caulerpa peltata* var. *nummularia* (J. Agardh) Weber van Bosse 1898: 376

Fig. 10

D. 13612, 13809. P. 2806, Parry Is. seaward reef, 3/6/55.

FIG. 10. *Caulerpa racemosa* var. *peltata* f. *nummularia*: Part of a plant of D. 13616b, × 4.5.

Caulerpa racemosa var. *macrophysa* (Kützing) Taylor; Dawson 1954: 393, fig. 10c; Dawson 1956: 35; Taylor 1950: 63

D. 13820. P. 1225, Parry Is. lagoon in 6 ft., 4/19/54.

Caulerpa racemosa (Forskål) J. Agardh near var. *uvifera* (Turner) Weber van Bosse 1898: 362, pl. 33, figs. 6, 7, 23; Taylor 1950: 63. *Fucus uvifer* Turner 1819: 81, pl. 230 (Red Sea)

D. 13635, 14006.

Caulerpa taxifolia (Vahl) C. Agardh; Dawson 1956: 35, fig. 17

D. 14046.

Caulerpa urvilliana Montagne; Taylor 1950: 60, pl. 31, figs. 1, 2, pl. 32, fig. 1; Dawson 1956: 37, fig. 21

D. 13607, 13632, 13674, 13757, 13818, 13845, 13862. P. 2824, Runo Is. seaward reef, 3/8/55; P. 2819, Bokanjoio Is. seaward reef, 3/8/55; P. 1225A, Parry Is. lagoon in 6 ft., 4/19/54. These specimens are variable, but for the most part approach the f. *tristicha* (J. Agardh) Weber van Bosse of the type variety of the species.

Caulerpa vickersiae Børgesen; Dawson 1956: 36, fig. 18; Dawson 1954: 392, fig. 9f (as *C. ambigua* Okam.)

D. 13617a, 13988a.

Codium arabicum Kützing; Dawson 1956: 38, fig. 24

D. 13947, 14004. P. 1220, Bogombogo Is. seaward flats, 4/15/54; P. 2831, off Igurin Is. in lagoon at 50 ft., 3/16/55.

Codium geppii O. C. Schmidt; Dawson 1954: 395, fig. 13 k; Dawson 1956: 39, fig. 26

D. 13722, 13951, 13926, 14003. P. 2593, Bogallua Is. lagoon, 2/11/55; P. 52–25, Aomon Is., 10/22/52.

Dr. Silva, in a personal communication, states that reef material of this plant collected by A. Conger and examined by him certainly belongs to the *C. geppii* complex, but is referable to *C. bulbopilum* Setchell, which he is about to decide to recognize in his monograph on *Codium*.

Codium edule Silva, mentioned by Odum and Odum (1955), has not been examined, but may be referable here.

Codium saccatum Okamura 1915: 145, pl. 135, figs. 1–5 (Futaye, Amakusa Island, Japan)

Fig. 11*a*

P. 2835, Bogombogo Is. on coral of tidal flats, 5/30/54. This plant agrees in size and shape and in the morphology of the utricles except for a slight development of alvaeolae in the utricle end-walls, not shown by Okamura for the type.

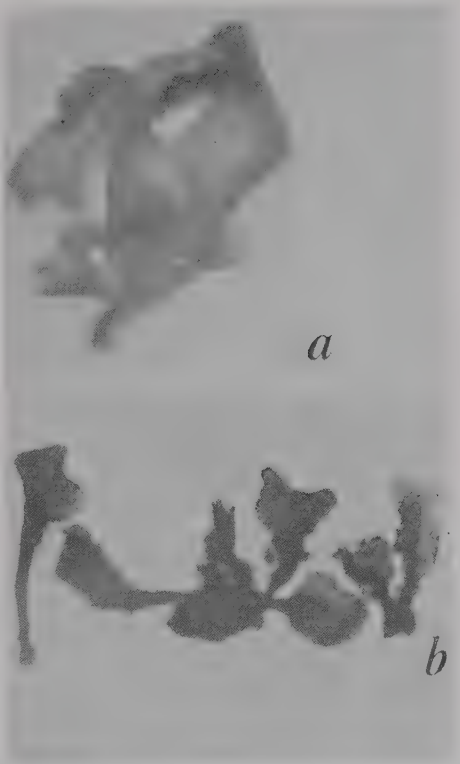


FIG. 11. *a*, *Codium saccatum*: A somewhat damaged plant of P. 2835, × 0.8. *b*, *Avrainvillea lacerata*: Habit of plants of D. 13629, × 1.05.

Codium tenue (Kützing) Kützing 1856, Tab. Phyc. 6: 33, pl. 95, fig. 1; Taylor 1950: 94. *Codium tomentosum* var. *tenue* Kützing 1849: 501 (Cape of Good Hope)

T. 46–436. Not collected again. Dr. Silva has reëxamined some preserved material of this collection and states in a personal communication that he considers it an undescribed species.

Pseudochlorodesmis furcellata (Zanardini) Børgesen; Dawson 1954: 395, fig. 11c

D. 13704b, 13987, 14048.

Avrainvillea lacerata Harvey ex J. Agardh 1887: 54 (Friendly Islands,-Tonga); A. and Ethel Gepp 1911: 38, figs. 105–109; Taylor 1950:70

Fig. 11*b*

D. 13629.

Rhipilia geppii Taylor 1950: 70, pl. 35 (Bikini Atoll, Marshall Islands)

D. 13721, 13889. P. 13x, Aaraanbiru Is. seaward reef margin, 3/7/54.

Rhipilia diaphana Taylor 1950: 72, pl. 37 (Bikini Atoll, Marshall Islands)

T. 46–425. Not collected again.

Rhipilia orientalis A. and Ethel Gepp; Taylor 1950: 72, pl. 36, fig. 1; Dawson 1956: 40

D. 13761, 13877, 13888.

Udotea palmetta var. *marshallensis* var. nov. Dawson 1956: 40, fig. 28a, b, c (as *U. palmetta*); Taylor 1950: 74 (as *U. indica*, at least in part)

Like the type, but the blade filament appendages in a single row, simple, blunt-conical, not forked.

A typo differt in appendiculis filamentae laminae in serie simplici efurcatis obtusiconicis.

TYPE: Dawson 13727, Aniyaanii Island, seaward reef on the coralline ridge, August 22, 1955.

ADDITIONAL MATERIAL: Kwajalein Atoll. D. 12554; Majuro Atoll. Horwitz 9576, 9599c, 9340a, 9390e; Eniwetok Atoll. T. 46–386, D. 13829, D. 13634, D. 13894, P. 2588a, Bogallua Is. lagoon rock pavement, 2/11/55, P. 54–33, Mui Is. seaward reef, 3/11/54, P. 2581a, Aaraanbiru Is. s.w. tip in channel, 2/11/55.

This considerable number of specimens has been found to show such consistent minor differences in the form of the blade filament appendages from the Indian Ocean type that there appears to be ample justification for its recognition under a distinctive subspecific name. One of Taylor's Eniwetok specimens referred by him to *U. indica* has been examined and found to be identical with the other Marshall Islands material. Presumably, his Rongerik, Rongelap and Bikini specimens treated as *U. indica* are also of this same plant.

Udotea javensis (Montagne) A. and Ethel Gepp; Dawson 1954: 395, fig. 13b, c; Dawson 1956: 40; Taylor 1950: 73

D. 13694, 13787, 13949.

Tydemannia expeditionis Weber van Bosse; Dawson 1956: 41; Taylor 1950: 73, pl. 38, fig. 1

D. 13962, 13997.

Halimeda gigas Taylor 1950: 84, pl. 44, fig. 2 (Eniwetok Atoll)

D. 13948, 13968, 13996. P. 1996, ½ mile off Parry Is. in lagoon at 140 ft., 9/9/54; P. 1947, ¼ mi. off Parry Is. in lagoon at 135 ft., 9/4/54; P. 2625, Parry Is. lagoon at 100 ft., 3/14/55; P. 2688, 1½ mile off Rigili Is. in lagoon at 60 ft., 3/16/55.

Halimeda macrophysa Askenasy 1888: 14, pl. 4, figs. 1–4 (Matuku Is., South Pacific); Barton 1901: 17, pl. 2, figs. 15–18

Fig. 12

D. 13879, 13897.

Halimeda monile (Solander) Lamouroux; Taylor 1950: 92, pl. 50, fig. 1; Dawson 1956: 41

D. 13706, 13836, 13937, 13953, 13969. P. 2828, 1½ mi. off Igurin Is. in lagoon at 50 ft., 3/8/55; P. 1993, ½ mi. off Parry Is. in lagoon at 140 ft., 9/9/54; P. 2687, 1½ mi. off Rigili Is. in lagoon at 60 ft., 3/16/55; P. 2620, 1½ mi. off Aaraanbiru Is. in lagoon at 70 ft., 3/11/55.

Halimeda lacunalis Taylor 1950: 91, pl. 51 (Eniwetok Atoll)

P. 2814, Bokanjoio Is. in lagoon off s.e. end of island at 60 ft., 3/8/55.

Halimeda stuposa Taylor 1950: 90, pl. 43, fig. 1, pl. 49, pl. 50, fig. 2 (Rongelap Atoll, Marshall Islands); Dawson 1956: 41

P. 2807, Parry Is. seaward reef edge, 3/6/55; P. 1200, Eneroul Is. lagoon, 4/14/54; P. 52–23, Aomon Is. lagoon at 5 ft., 10/22/52; P. 2588, Bogallua Is. lagoon rock pavement, 2/11/55.

Halimeda fragilis Taylor 1950: 88, pl. 48, fig. 2; Dawson 1956: 41

T. 46–394. Not collected again.

Halimeda opuntia (Linnaeus) Lamouroux; Taylor 1950: 80, pl. 39, fig. 1; Dawson 1954: 395, fig. 12; 1956: 41

D. 13631, 13700, 13734, 13796. P. 2529, 2530, ¼ mi. off Aaraanbiru Is. in lagoon at 20 ft., 3/9/55.

Halimeda opuntia f. *hederacea* Barton 1901: 21, pl. 3, fig. 23 (East Indies); Taylor 1950: 81, pl. 40, fig. 1; Dawson 1956: 42

D. 13954, 13998. P. 1950, ¼ mi. off Parry Is. in lagoon at 135 ft., 9/4/54.

Halimeda opuntia f. *minima* Taylor 1950: 82, pl. 39, fig. 2 (Bikini Atoll, Marshall Islands)

D. 14001.

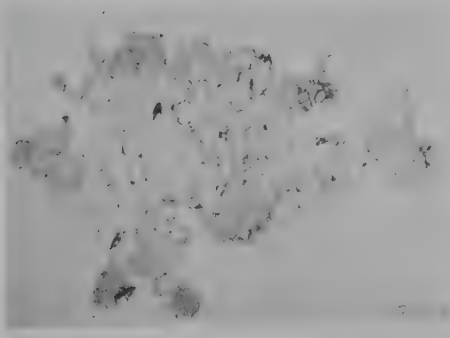


FIG. 12. *Halimeda macrophysa*: Habit of a plant of D. 13879, × 0.5.

Halimeda opuntia f. *triloba* (Decaisne) Barton 1901: 20, pl. 2, fig. 20; Taylor 1950: 81, pl. 40, fig. 2. *Halimeda triloba* Decaisne 1842: 90 (China Sea)

D. 14001a. P. 2618, 1 mi. off Aaraanbiru Is. in the lagoon at 70 ft., 3/11/55.

Halimeda taenicola Taylor 1950: 86, pl. 46, fig. 1; Dawson 1956: 42

D. 13759.

Halimeda tridens f. *lamourouxii* (J. Agardh) Weber van Bosse; Taylor 1950: 93. *Halimeda incrassata* var. *lamourouxii* J. Agardh 1887: 86 ("in mari Antillarum"); Barton 1901: 27, pl. 4, fig. 41

Fig. 13

D. 14044.

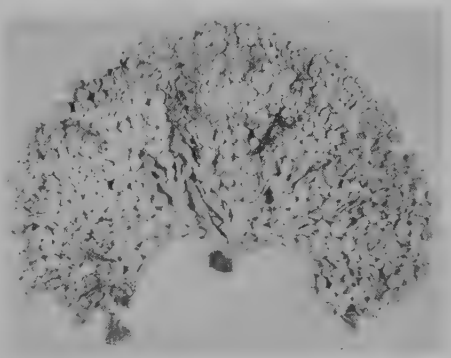


FIG. 13. *Halimeda tridens* f. *lamourouxii*: Habit of a plant of D. 14044, × 0.45.

Ostreobium reineckii Reinbold; Dawson 1954: 396, fig. 13g

D. 13776a, growing in the calcareous material of the lower side of *Peyssonelia rubra* var. *orientalis*.

Neomeris bilimbata Koster; Dawson 1956: 42, fig. 30a, b

D. 13772. Taylor's number 46–557 from Rongerik Atoll has been reëxamined and found to agree with this species rather than with *Neomeris vanbosseae* Howe.

Acetabularia moebii Solms-Laubach; Dawson 1954: 397, fig. 13j; Dawson 1956: 43
D. 13617b, 13660, 13858.

BROWN ALGAE

Ectocarpus breviarticulatus J. Agardh; Dawson 1954: 398, fig. 14a, b; Dawson 1956: 43
D. 13620, 14037. P. 2803, Bokanjoio Is. seaward reef margin, 10/25/54; P. 2804, Parry Is. seaward reef flats, 2/5/55.

Ectocarpus indicus Sonder, in Zollinger; Dawson 1956: 43, fig. 32; Taylor 1950: 95
D. 13766, epiphytic on *Turbinaria*, 13950, epiphytic on *Halimeda* and *Caulerpa*, 13959.

Ectocarpus irregularis Kützing; Dawson 1954: 398, fig. 14e, f; Børgesen 1941: 23, figs. 8–11
P. 2854a, epiphytic on *Dictyota*, Bogallua Is. lagoon pavement, 11/17/54.

Ectocarpus mitchellae Harvey; Taylor 1950: 95; Dawson 1954: 400, fig. 14c, d; Dawson 1956: 43; Børgesen 1941: 7, figs. 1–5
D. 13979.

Sphacelaria furcigera Kützing; Dawson 1954: 400, fig. 14h; Dawson 1956: 44
D. 13696a.

Sphacelaria novae-hollandiae G. Sonder; Dawson 1954: 400, fig. 14g; Taylor 1950: 97
D. 13748, 13768, 13936, all epiphytic on *Turbinaria*.

Sphacelaria tribuloides Meneghini; Dawson 1954: 400, fig. 14i, j; Dawson 1956: 44
D. 13622. P. 2812, Bokanjoio Is. lagoon on stake in 3 to 8 feet of water, 3/8/55.

Pocockiella papenfussii Taylor 1950: 98, pl. 54, fig. 2; Dawson 1956: 44
D. 13720. P. 54–31, Mui Is. seaward reef under rocks, 3/11/54.

Pocockiella variegata (Lamouroux) Papenfuss; Dawson 1954: 400, fig. 14k; Dawson 1956: 44
D. 13775, 13866.

Dictyota divaricata Lamouroux 1809: 331 (Mediterranean coast of France); Taylor 1928: pl. 16, figs. 6–9; Taylor 1950: 101

Fig. 14*a*

D. 13614 (juvenile), 13691, 13883, 13898. P. 2690, 1½ mi. off Rigili Is. at 60 ft., 3/16/55.

Dictyota patens J. Agardh; Dawson 1954: 401, fig. 16c
D. 13938. P. 2854, Bogallua Is. lagoon pavement, 11/17/54.

Dictyota pinnatifida Kützing 1859, Tab. Phyc. IX: 16, pl. 39 (Antigua, West Indies); Taylor 1950: 100
T. 46–416. Not collected again.

Dictyopteris repens (Okamura) Børgesen; Dawson 1956: 44, fig. 34
D. 13611, 13749.

Padina australis Hauck 1887: 44 (Cape York, North Australia); Weber van Bosse 1913: 179, fig. 52

Fig. 14*b*

D. 13678.

Padina commersonii Bory; Dawson 1954: 401, fig. 17; Taylor 1950: 100, pl. 54, fig. 1; Dawson 1956: 44
D. 13830, 14045. In this species the fertile zones alternate with hair zones, while in *P. australis* each fertile zone has a hair zone on either side separated from the next hair zone by a sterile zone.

Hydroclathrus clathratus (Bory) Howe; Dawson 1954: 403, fig. 18b; Taylor 1950: 96
D. 13918, 14021. P. 2845, Bokanjoio Is. seaward boat passage in 6 ft., 9/30/54.

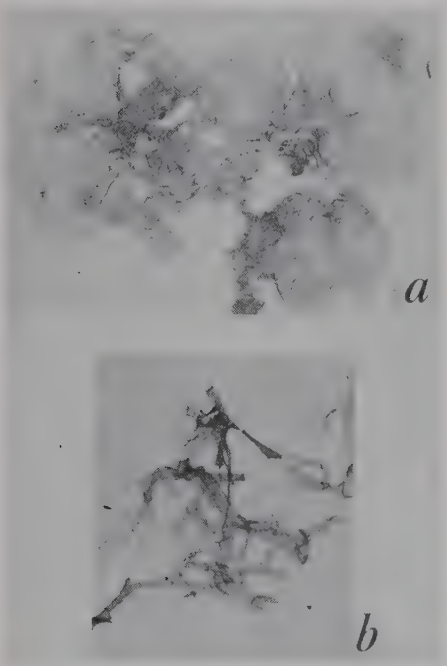


FIG. 14. *a*, *Padina australis*: Habit of a plant of D. 13678, × 0.8. *b*, *Dictyota divaricata*: Habit of parts of plants of D. 13691 showing great attenuation of some segments, × 0.7.

Rosenvingea intricata (J. Agardh) Børgesen 1914: 181; Taylor 1950: 97 *Asperococcus intricatus* J. Agardh 1847: 7 (Vera Cruz, Mexico)

Fig. 15

D. 13919. Rather dwarfish material which most closely resembles plants from the Gulf of California (Dawson 1944).

Rosenvingea fastigiata (Zanardini) Børgesen 1914: 26; Taylor 1950: 96, pl. 52, fig. 2. *Asperococcus fastigiatus* Zanardini 1872: 134, pl. 3, figs. 1–3 (Sarawak)
T. 46–332. Not collected again.

Chnoospora implexa Hering ex J. Agardh; Dawson 1954: 404, fig. 20a, b
D. 14022. P. 1195, Bokanjoio Is., seaward reef margin, 4/14/54.

Turbinaria ornata (Turner) J. Agardh; Dawson 1954: 405, fig. 21; Dawson 1956: 44; Taylor 1950: 100, pl. 53, fig. 2, pl. 55, fig. 2
D. 13693, 13765, 13802, 13935.

RED ALGAE

Goniotrichum elegans (Chauvin) Zanardini 1847: 69. *Bangia elegans* Chauvin 1842: 32 (Arromanches, France). Taylor 1950: 117 (as *G. alsidii* (Zanard.) Howe)

Fig. 16*a*, *b*

D. 13696e, epiphytic on a bit of *Cladophora* among other small algae in mixture.

Asterocytis ornata (C. Agardh) Hamel; Dawson 1954: 411, fig. 23a; Taylor 1950: 116
T. 46–427. Not detected again.

Erythrotrichia carnea (Dillwyn) J. Agardh; Dawson 1956: 45; Taylor 1950: 117; Tanaka 1952: 14, fig. 7B–E

Fig. 16*c*

D. 13906a.

Erythrotrichia parietalis Tanaka; Dawson 1954: 412, fig. 23d, e
D. 13696c.

Acrochaetium gracile Børgesen; Dawson 1954: 414, fig. 25h, i

Fig. 17*b*

D. 13696b, epiphytic on *Lophosiphonia* and

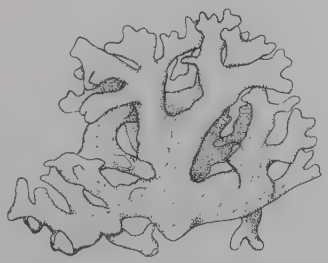


FIG. 15. *Rosenvingea intricata*: Habit of part of a small plant of D. 13919, × 3.7.

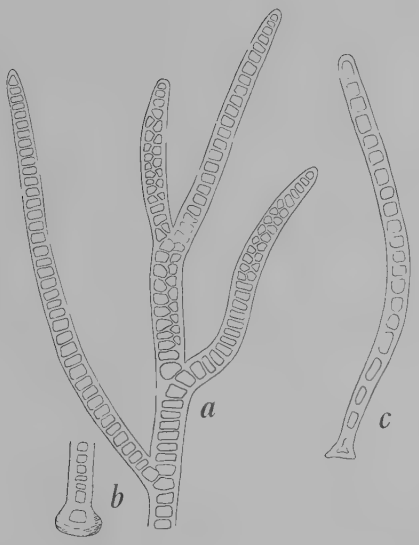


FIG. 16. *a, b, Goniotrichum elegans*: *a*, Habit of the upper part of a plant; *b*, basal part of same, both × 150 (after Børgesen). *c, Erythrotrichia carnea*: Habit of a young plant, × 300 (after Tanaka).

other small algae. This material seems to agree even better with the original account than the Viêt Nam specimens cited above. Attenuated hairs are common.

Acrochaetium robustum Børgesen; Dawson 1954: 414, fig. 25j, k
P. 2847, Bokanjoio Is. lagoon on *Enteromorpha*, 9/29/54.

Kylinia crassipes (Børgesen) Kylin 1944: 13. *Acrochaetium crassipes* Børgesen 1915: 20, figs. 11–13 (Virgin Islands)

Fig. 17*a*

D. 13620b, epiphytic on small algae.

Kylinia secundata (Lyngbye) Papenfuss 1947: 437. *Callithamnion daviesii* var. *secundatum* Lyngbye 1819: 129 (Denmark)

Fig. 17*c, d*

D. 13976b. Rather scant material, but fertile and in general agreement with the species as interpreted by the writer in 1953.

Liagora farinosa Lamouroux; Dawson 1954: 415, figs. 25d, 26; Taylor 1950: 119
P. 2820, Bokanjoio Is. seaward reef edge, 3/8/55.

Liagora hawaiiana Butters 1911: 164, pl. 24, figs. 8, 9 (Laie Bay, Oahu, Hawaiian Islands); Taylor 1950: 119, pl. 57, fig. 1; Abbott 1945: 151, fig. 3
D. 13828.

Liagora orientalis J. Agardh; Dawson 1954: 415, fig. 27b

Fig. 19*a, b*

A. Conger 4/27/51, Lidilibut Is., among coral heads in sandy channels on the ocean side. Principal specimen in the Bishop Museum. The material is sterile and is not positively identified.

Liagora pinnata Harvey 1853: 138, pl. 31 B, figs. 1–5 (Sand Key, Florida); Abbott 1945: 168

Fig. 18

P. 54–19, Aitsu Is., seaward reef near edge, 3/10/54.

Liagora robusta Yamada 1938: 8, pl. 12, fig. 1, text figs. 3, 4 (Ogasawara Islands)

Fig. 19*c, d*

A. Conger 4/27/51, Lidilibut Is. in sandy channels on the ocean reef side. Sterile and not positively identified.

Asparagopsis taxiformis (Delile) Collins and Hervey 1917: 117. *Fucus taxiformis* Delile 1813: 295, pl. 57, fig. 2 (Alexandria, Egypt)

Fig. 20

D. 13627, 13843, 14018. P. 16, Japtan Is. seaward reef, 8/8/49; P. 2601a, Rigili Is., 2/11/55; P. 2501, Engebi Is. lagoon at n.w. tip in 15 ft., 3/2/55.

FIG. 17. *a*, *Kylinia crassipes*: Habit of a plant, × 290. *b*, *Acrochaetium gracile*: Habit of part of a plant, × 150 (after Børgesen). *c*, *d*, *Kylinia secundata*: *c*, Habit of the upper part of a plant, × 160; *d*, detail of stellate chromatophores in part of a filament, × 1000 (after Dawson).

Falkenbergia hillebrandii (Bornet) Falkenberg = sporophyte generation of *Asparagopsis taxiformis* (Delile) Collins and Hervey; Dawson 1954: 414, fig. 25l; Dawson 1956: 45

D. 13623, 13913, 14018a. P. 2836b, Parry Is. seaward reef edge, 4/4/54.

Galaxaura fastigiata Decaisne; Dawson 1954: 419, fig. 30b

P. 2805, Bogombogo Is. seaward reef flats, 2/9/55.

Galaxaura filamentosa Chou; Dawson 1954: 419, fig. 30a; Dawson 1956: 46

D. 14005. Rather scant, young material.

Gelidium crinale var. *perpusillum* Piccone and Grunow; Dawson 1954: 421, fig. 31e, f

D. 13798.

Gelidium pusillum (Stackhouse) Le Jolis, formas; Dawson 1954: 420, fig. 31a–c; Dawson 1956: 46

D. 13819, 13841.

Gelidiella bornetii (Weber van Bosse) Feldmann and Hamel 1934: 528; Børgesen 1938: 210, fig. 2a, b. *Gelidium bornetii* Weber van Bosse 1926: 107 (Kei Islands)

Fig. 21

D. 14035 is a good match for Børgesen's 1938 figure. The small size and compressed to flattened branches lacking rhizoidal filaments are distinctive.

Gelidiella tenuissima Feldmann and Hamel; Dawson 1954: 422, fig. 33e; Dawson 1956: 46

D. 13660a, 13908, 14032.

Gelidiopsis intricata (C. Agardh) Vickers; Dawson 1954: 423, fig. 34a–d; Dawson 1956: 46

D. 13903.

Wurdemannia miniata (Lamark and DeCandelle) Feldmann and Hamel: Dawson 1954: 424, fig. 35; Dawson 1956: 47

D. 13640b, 14036.

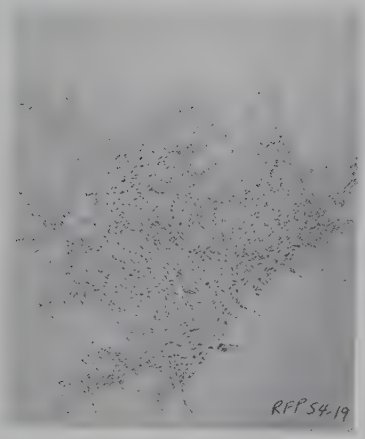


FIG. 18. *Liagora pinnata*: Habit of a dry specimen of P. 54–19, × 0.65.

Cruoriella dubyi (Crouan and Crouan) Schmitz; Dawson 1956: 47, fig. 39
D. 13856.

Peyssonelia rubra var. *orientalis* Weber van Bosse; Dawson 1954: 424, fig. 36c; Dawson 1956: 47; Taylor 1950: 121
D. 13776, 13991.

Porolithon craspedium (Foslie) Foslie 1909: 57; Taylor 1950: 126, pls. 64, 65. *Lithophyllum craspedium* Foslie 1900: 26 (Onatoa, Gilbert Islands)
D. 13717, 13943.

Porolithon oncodes (Heydrich) Foslie 1909: 57; Taylor 1950: 125, pls. 9, 61, 62, 63. *Lithophyllum oncodes* Heydrich 1897: 410 (Tami Island, New Guinea)
D. 13618, 13869, 14019.

Porolithon gardneri f. *subhemispherica* Foslie 1907: 190 (Indian Ocean); Taylor 1950: 129, pls. 5–9, 70, fig. 1; pls. 71–73, 76, fig. 2; pl. 77
T. 46–373, T. 46–306, T. 46–406. Not collected again since 1946.

Fosliella farinosa (Lamouroux) Howe; Dawson 1954: 425, fig. 37c; Taylor 1950: 132 (as *F. farinosa* var. *solmsiana* (Falkenb.) Taylor, prox.
D. 13720a, epiphytic on *Pocockiella*.

Heteroderma minutula Foslie; Dawson 1956: 47, fig. 40
D. 13719a, 13821, both epiphytic on *Dictyosphaeria intermedia*; D. 13994a, epiphytic on *Valonia*.

Heteroderma subtillissima Foslie; Dawson 1956: 48, fig. 41a, b
D. 13857b, in *Jania* turf; D. 13818, epiphytic on *Caulerpa urvilliana*.

Jania capillacea Harvey; Dawson 1954: 432, fig. 41a, b; Dawson 1956: 49; Taylor 1950: 133
D. 13640, 13649, 13692. P. 2858, Runit Is. in channel at n.w. tip, 4/11/54.

Jania decussato-dichotoma (Yendo) Yendo; Dawson 1956: 49, fig. 44
D. 13769, 13805, 13910. The specimens cited by Taylor 1950: 133 under *Jania rubens* Lamx. are presumed to correspond with this common Pacific species.

Jania micrarthrodia Lamouroux; Dawson 1956: 49, fig. 42; Taylor 1950: 134 (as *J. antennina* Kützing, prox.)
T. 46–345B. Not collected again.

Jania tenella Kützing; Dawson 1956: 49, fig. 43
P. 2836a, Parry Is. seaward reef edge, 4/4/54; P. 2860, same, 3/10/54.

Grateloupia filicina (Wulfen) C. Agardh; Dawson 1954: 432, fig. 42a
D. 13972. P. 2837, same locality, 5/29/54.

Hypnea esperi Bory; Dawson 1954: 436, fig. 46h–j; Dawson 1956: 51
D. 13617, 13697, 13788, 13852, 13814, 13902, 13939, 14015. Taylor's Eniwetok col-

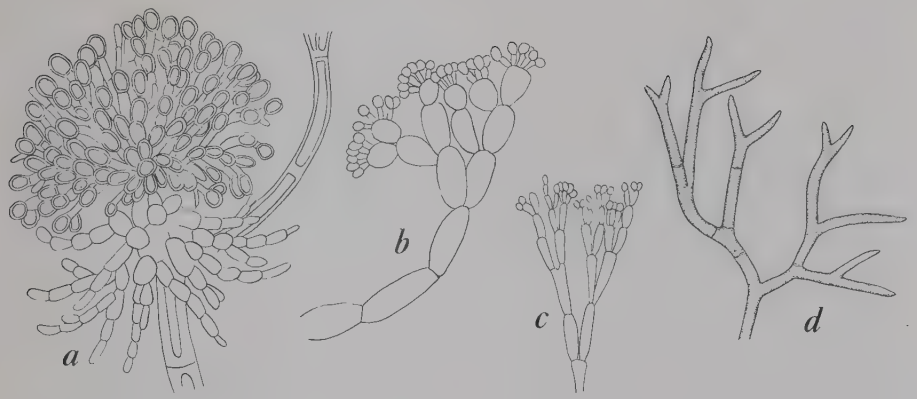


Fig. 19. *a*, *b*, *Liagora orientalis: a*, A young cystocarp, × 300; *b*, an antheridial branch, × 470 (both after Yamada). *c*, *d*, *Liagora robusta: a*, An antheridial branch, × 350 (after Yamada); *b*, part of a plant of Conger 4/27/51 showing the open dichotomous branching and annulations, × 1.5.

Fig. 20. *Asparagopsis taxiformis*: Habit of dry plants typical of the small reef form, × 1.15.

lection of *Hypnea* under no. 46–378 called *H. spinella* (Ag.) Kütz. is probably the same as these.

Hypnea nidulans Setchell; Dawson 1954: 438, fig. 46e–g
D. 13861.

Hypnea pannosa J. Agardh; Dawson 1956: 51, fig. 46
D. 13912.

Dicranema rosaliae Setchell and Gardner 1924: 745, pl. 22, fig. 6 (Gulf of California, Mexico)
Figs. 22*a;* 23*a*
D. 13980.

Botryocladia skottsbergii (Børgesen) Levring; Dawson 1956: 52, fig. 48; Taylor 1950: 135 (as *Botryocladia kuckuckii* Weber van Bosse) Yamada and Tanaka
D. 13986, 14033.

Coelothrix irregularis (Harvey) Børgesen 1915–20: 389, figs. 373, 374. *Cordylecladia ? irregularis* Harvey 1853: 156 (Key West, Florida)
Fig. 23*b*

D. 13782. The tetrasporic material agrees exactly with Harvey. It is probably identical also with *C. indica* Børgesen from Mauritius which seems doubtfully distinct in view of this Pacific record. The species is probably widespread in tropical waters but of infrequent occurrence in the Pacific and Indian Ocean regions.

FIG. 21. *Gelidiella bornetii*: Habit of part of a plant of D. 14035, × 9.

Lomentaria hakodatensis Yendo; Dawson 1956: 52, fig. 50
D. 13709, 13853, 13928, 13999i, 14025.

Champia parvula (C. Agardh) Harvey; Dawson 1954: 443, fig. 52c; Dawson 1956: 51
D. 13746, 13849, 14015a.

Champia vieilardii Kützing ?; Dawson 1954: 443, figs. 52e, 53; Dawson 1956: 51
D. 13999f. A small fragment only of uncertain identity.

Rhodymenia anastomosans Weber van Bosse; Dawson 1956: 52, fig. 49
D. 13900.

Antithamnion lherminieri (Crouan and Crouan) Nasr; Dawson 1956: 53, fig. 51
D. 13609a, creeping among other minute algae; 13696b, 13950b, epiphytic on *Halimeda* and *Caulerpa;* 13999b, epiphytic on *Halimeda*.

Antithamnion percurrens sp. nov.

Fig. 24*a*, *b*

Thalli minute, densely tufted, 5–6 mm. high, uniseriate throughout; creeping, prostrate filaments of lower parts fastened to the calcareous substrate by short lateral branchlets modified for attachment; main axes both prostrate and erect about 15–18 μ in diameter, of cells mostly 2–3 diameters long; erect axes strongly percurrent, without indeterminate branches; determinate lateral branchlets regularly distichous from every axial cell, 60–120 μ long, symmetrically curved upward, commonly bearing 1–3 short, 1–2 celled secondary determinate branchlets on the adaxial side; all branch tips blunt; tetrasporangia about 20 μ in diameter, tripartite, sparse, sessile, borne within a large, prominent, gelatinous envelope from the adaxial side of the basalmost cell of a lateral branchlet, usually causing a local disarrangement of the pinnae because of the size of the envelope.

Thallis 5–6 mm. altis in omnis partibus uniseriatis, axilibus principalibus valde percurrentibus 15–18 μ diametro cellulis plerumque 2–3-plo longioribus quam latis,

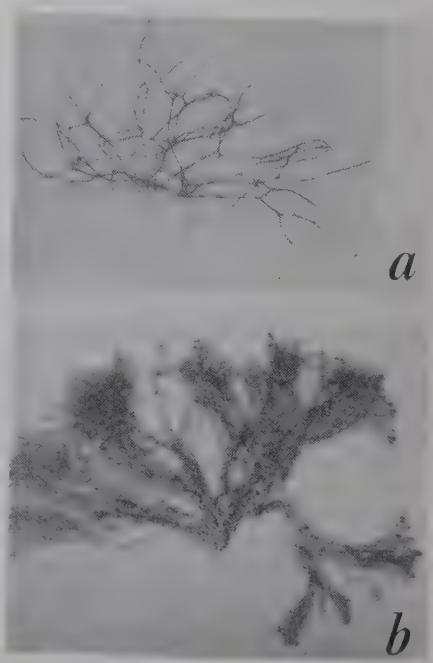


FIG. 22. *a*, *Dicranema rosaliae*: Habit of a dry plant of D. 13980, × 1.7. *b*, *Dasya iyengarii*: Habit of part of a dried tuft of a somewhat robust form, × 2.0.

FIG. 23. *a*, *Dicranema rosaliae*: Transection of a branch to show central core of small cells (after Setchell and Gardner). *b*, *Coelothrix irregularis*: Habit of part of a tetrasporic plant of D. 13782 with stichidia, × 10.

ramulis lateralibus determinantibus regulariter distichis ex cellulis axilaribus omnibus salientibus 60–120 μ longis adscendenti-curvatis et in latere adaxilare ramulis determinantibus secundariis productis, apicibus ramorum obtusis, tetrasporangiis ca. 20 μ diametro tripartitis sessilibus sparsis e latere adaxiali cellulae inferioris ramulis lateralibus productis.

TYPE: Dawson 13633, forming tufts on crustose coralline algae near the outer margin of the seaward reef opposite EMBL, Parry Island, August 19, 1955.

This plant is related to *Antithamnion pteroton* Schousb. ex Bornet, but is a markedly distinct species in its percurrent erect axes, its large, sessile sporangia, and the short, symmetrical pinnae lacking any abaxial secondary branchlets.

Antithamnion breviramosus* var. *simplex var. nov.

Fig. 24*c*, *d*

Like the type, but more delicate and slender with main axes only 25–30 μ in diameter, and with lateral branchlets simple or only once forked; axial cells longer, 6–8 (10) diameters long; attachment by a short, 1–2 celled rhizoidal outgrowth from the lowermost cell of a lateral branch.

A typo simili sed axilibus principalibus tantum 25–30 μ diametro et cellulis longioribus 6–8 (10)-plo longioribus quam latis, ramulis lateralibus simplicibus vel unifurcatis.

TYPE: Dawson 13704a, creeping on *Griffithsia tenuis* from coral heads at a depth of 10 feet in the lagoon, south end of Parry Island, August 21.

This tiny plant is remarkably similar to that described from Santa Catalina Island, California (Dawson 1949: 14, figs. 28, 57) and seems to be only a more delicate, lax, and less-branched variant of that species.

Callithamnion marshallensis sp. nov.

Fig. 25*a–c*

Thalli attached to other algae or to shells or debris, loosely tufted, 4–5 mm. high, consisting of an irregularly semi-prostrate part attached by modified lateral branchlets with adherent terminal discs, some of the attachment branchlets distinctly catenate in their cell form and unlike vegetative branchlets; main axes 80–90 μ in diameter, noncorticated, of cells 1–1½ diameters long; lateral branchlets 20–30 μ in diameter, lax, long, somewhat attenuate but terminally blunt, mostly simple, curved, alternate, but not always from every cell, mostly spirally arranged; often with approximately ⅕ divergence, but sometimes in part tending to be distichous; tetrasporangia tripartite, subspherical, about 40 μ in diameter, sessile and

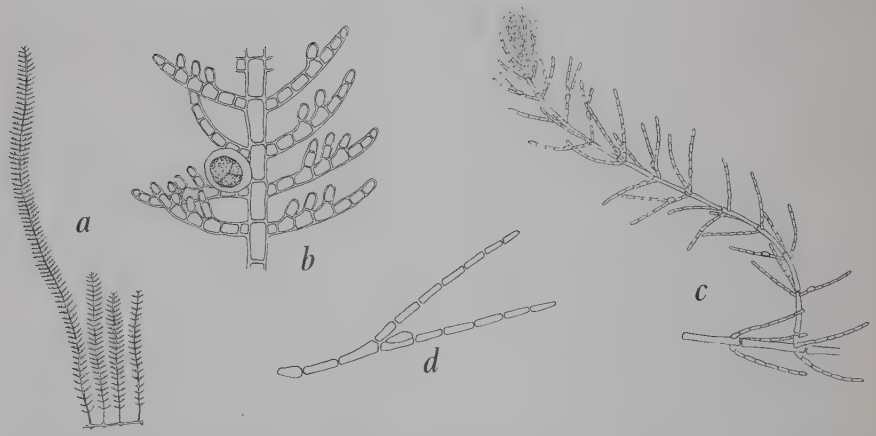


FIG. 24. *a*, *b*, *Antithamnion percurrens: a*, Habit of part of a plant of the type collection, × 13; *b*, part of a plant bearing a tetrasporangium, × 150. *c*, *d*, *Antithamnion breviramosus* var. *simplex: c*, Habit of part of a plant of the type collection, × 68; *d*, detail of an ultimate forked branch bearing a gland cell, × 300.

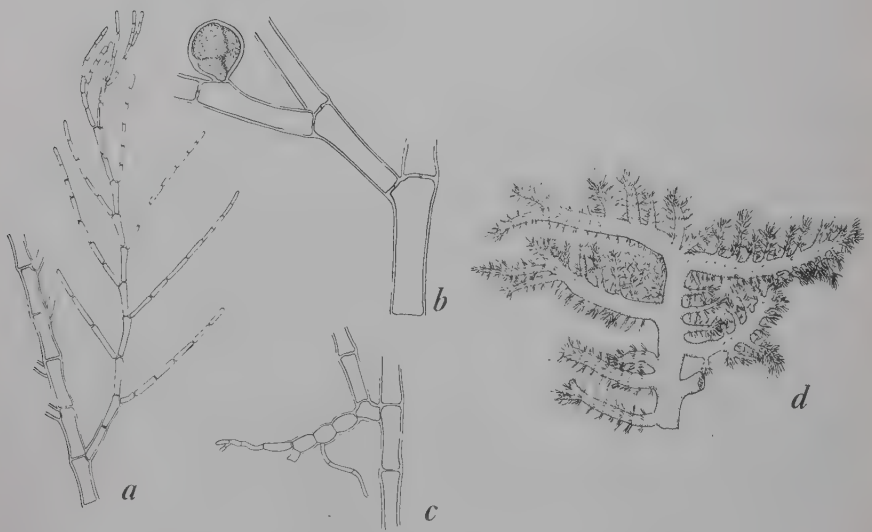


FIG. 25. *a–c*, *Callithamnion marshallensis: a*, Part of a plant of D. 13698a to show branching habit, × 70; *b*, detail of a branch bearing a tetrasporangium, × 162; *c*, detail of a lower part of a plant showing a catenate holdfast branch, × 60. *d*, *Wrangelia anastomosans:* Habit of part of a plant of P. 79a, as seen from the lower side, × 3.

adaxial, one or several in the lower half of a lateral branchlet in mid-parts of thallus.

Thallis 4–5 mm. altis, partibus inferis semiprostratis a ramulis lateralibus mutatis in discis adhaerentibus, axilis principalibus 80–90 μ diametro ecorticatis et cellulis 1–1½-plo longioribus quam latis, ramulis lateralibus 20–30 μ diametro laxis subattenuatis sed obtusis plerumque simplicibus curvatis alternatis plerumque contorte affixis, tetrasporangiis tripartitis ca. 40 μ diametro sessilibus adaxialibus in dimidia parte infera ramulae lateralis in media thalli affixis.

TYPE: Dawson 13695, on shells and dead coral from a depth of 6–10 feet in the lagoon, south end of Parry Island, Eniwetok Atoll, August 21.

ADDITIONAL MATERIAL: D. 13992, under rocks on reef along passage; D. 13950a, epiphytic on *Halimeda* and *Caulerpa*; D. 13997c, epiphytic on *Halimeda*; D. 13698a.

This species is seemingly nearest to *Callithamnion paschalis* Børgesen (1924: 294, fig. 35) from Easter Island, but is neither consistently distichously branched like that species nor with the tetrasporangia borne in the terminal branchlets of the main axes.

Wrangelia anastomosans Yamada 1944: 41, pl. 7, fig. 2 (Ant Atoll, Caroline Islands)

Fig. 25*d*

P. 79a, Igurin Is. tide flats in shallow water, 11/4/54.

Wrangelia argus (Montagne) Montagne; Dawson 1954: 444, fig. 54g; Dawson 1956: 56

D. 13941. This material agrees with the details by which Tseng (1942) differentiates *W. argus* from *W. tayloriana* Tseng, and lacks the more or less complete cortication of *W. penicillata*. The involucral filaments are about 11–13 μ in diameter, of 3 to 5 cells, often dichotomous and strongly curved. The tetrasporangia are 70–80 μ in diameter at maturity.

Wrangelia penicillata C. Agardh 1828: 138 (Adriatic Sea); Taylor 1950: 136

T. 46–336. Not collected again.

Griffithsia ovalis Harvey 1862, vol. 4: pl. 203 (King Georges Sound, West Australia); Abbott 1946: 440, pl. 1, figs. 1–4, pl. 2, figs. 1, 2

Fig. 26*a–d*

D. 14012, fertile. Several other sterile collections were made of a *Griffithsia* which is probably this species.

Griffithsia tenuis C. Agardh; Dawson 1954: 450, fig. 56e; Dawson 1956: 56

D. 13702, 13785, 13950d, 13956, 14029.

Neomonospora pedicellata var. *tenuis* Feldmann-Mazoyer; Dawson 1954: 450, fig. 56a

D. 13610a.

Ceramium clarionense Setchell and Gardner; Dawson 1954: 448, fig. 55k; Dawson 1956: 54

D. 13767. This material, epiphytic on *Turbinaria*, is sterile, but the circinate tips and

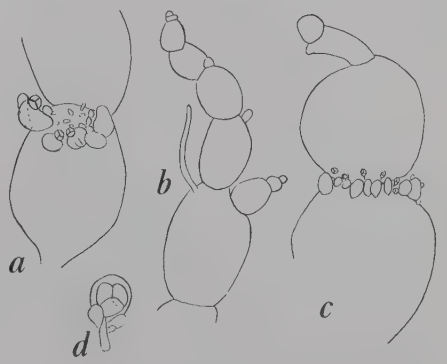


FIG. 26. *a–d*, *Griffithsia ovalis*: *a*, Vegetative cells with involucrate tetrasporangia between articulations, × 30; *b*, habit of part of a specimen with a rhizoid, × 16; *c*, involucrate tetrasporangia near the top of a plant, × 26; *d*, a mature tetrasporangium on a pedicel, × 300 (all after Abbott).

the peculiar exudation droplets from certain cortical cells seem to mark it clearly.

Ceramium marshallense sp. nov.

Fig. 27*a*, *b*

Thalli creeping and entangled among other algae in low turfs, 1 cm. or less in extent, consisting of creeping lower parts fastened to surrounding materials by numerous rhizoids, and free branches 4–5 mm. long; branching primarily dichotomous, with occasional irregular secondary branches; sterile apices strongly forcipate and usually circinately inrolled; main axes to 140–155 μ in diameter; cortication incomplete, consisting of nodal bands about 50–60 μ wide separating uncorticated internodal areas 40–70 μ wide; cortical bands consisting of a central ring of larger, isodiametrical cells about 22–30 μ in diameter and on either side, or somewhat overlapping, an irregular single to double ring of smaller angular cells 10–17 μ in greatest diameter; fertile, outer, erect parts of tetrasporangial plants somewhat catenately swollen, 160–185 μ in diameter; tetrasporangia mostly completely immersed beneath the tumid cortex, 35–40 μ in diameter, whorled after an initial tendency to be abaxial; sexual reproduction unknown.

Thallis repentibus et implicatis ad 1 cm. longis a rhizoideis multis affixis, ramis solutis 4–5 mm. longis, ramulis plerumque dichotomis, apicibus circinatis, axilibus principalibus 140–155 μ diametro, cortice interrupta, vittis corticalibus noduloris ca. 50–60 μ latis

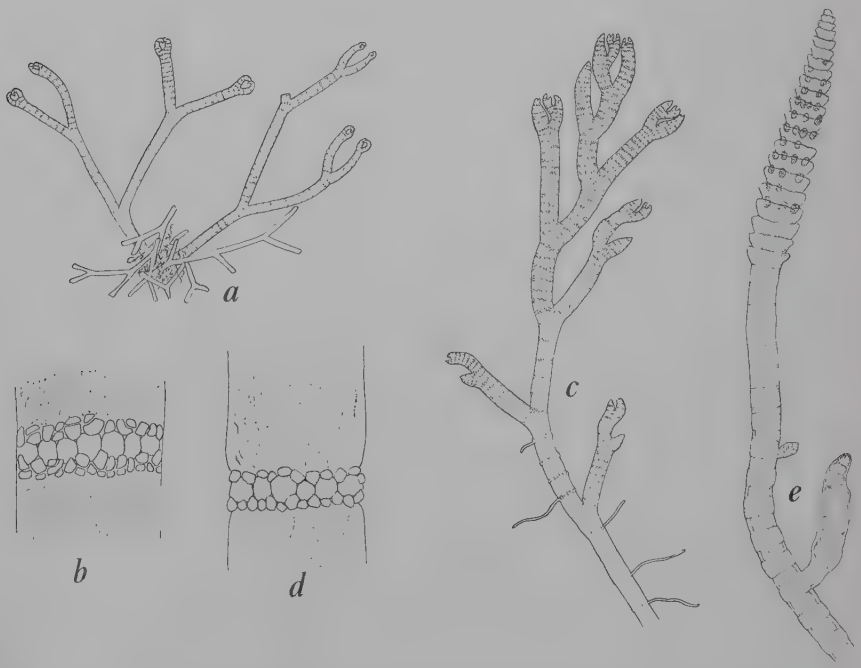


FIG. 27. *a*, *b*, *Ceramium marshallense: a*, Habit of a plant of the type collection, × 12; *b*, detail of a node of the same, × 150. *c*, *d*, *Ceramium sympodiale: c*, Habit of a plant of the type collection, × 26; *d*, detail of a node of the same, × 150. *e*, *Ceramium vagabunde:* Habit of the upper part of a tetrasporangial plant of the type collection, × 34.

a circulo unico cellulis majoribus 22–30 μ diametro et in lateribus ambis circulo irregulari cellulis minoribus angulosis 10–17 μ diametro, internodis 40–70 μ latis, tetrasporangiis 35–40 μ diametro verticillatis plerumque tota immersis sub cortice tumidi.

TYPE: Dawson 14013, growing in a *Jania* turf among rocks near the northern seaward reef edge of Rigili Island, Sept. 2.

This species is distinct in its small size, circinate apices, narrow cortical bands less than one-half as tall as broad, and in its immersed, whorled tetrasporangia. It approaches *C. mazatlanense* Dawson, but differs in the cellular arrangement of the cortical bands and in the whorled, immersed tetrasporangia.

Ceramium sympodiale sp. nov.

Fig. 27*c*, *d*

Thalli 1 cm. or less in height or extent, with main axes 110–130 μ in diameter, consisting of repent or entangled lower parts growing amid other small algae in tufts or turfs, attached at many places by rhizoids from the nodes, giving rise to erect, free parts 3–4 mm. high; branching sympodial and essentially distichous, the branches approximate above and becoming more widely spaced below by elongation of the internodes; branches at extreme apices at first more or less corymbose and the tips slightly forcipate with clearly visible apical cells; cortication incomplete, in narrow bands 35–40 μ wide (⅓ the diameter of the axis or less), consisting of a single ring of larger cells about 30–35 μ in diameter with smaller, angular cells on either side; internodes very narrow in upper parts, about 10 μ wide, expanding below to as much as 170 μ; reproduction not seen.

Thallis ad 1 cm. latis, axilibus principalibus 110–130 μ diametro, partibus inferis repentibus a rhizoideis noduloris affixis, partibus solutis 3–4 mm. altis, ramis sympodialibus et plerumque distichis ad apices corymbosis, apicibus subforcipatis, cortice interrupti vittis corticosis nodi 35–40 μ latis a circulo unico cellulis majoribus 30–35 μ diametro et in lateribus ambis cellulis minoribus anguloris, inter nodis supra angustioribus ca. 10 μ latis infra latioribus ad 170 μ latis.

TYPE: Dawson 14014, in clumps of other small algae under coral rocks near the northern edge of the seaward reef of Rigili Island, September 2.

The sympodial, distichous branching and very narrow cortical bands are distinctive in this small species despite the absence of fertile material.

Ceramium vagabunde sp. nov.

Fig. 27*e*

Plants minute, 4–5 mm. high, growing among other tufted algae, consisting of a creeping, semi-prostrate basal filament provided with numerous ventral rhizoids from the nodes, giving rise to irregularly and sparsely branched erect branches with blunt, non-forcipate tips; erect axes 120–140 μ in diameter, incompletely corticated, the internodes bare for intervals of 30–70 μ in middle and lower parts; cortical bands 1½–2 times as broad as tall, without secondary growth above or below, the margins even, especially the lower ones, consisting of a narrow inner ring of larger cells and on either side of an outer ring of irregularly arranged small angular cells less than 10 μ in maximum diameter; tetrasporangia cruciate, ovate, about 40 μ in length, borne verticillately within prominently swollen involucres which develop acropetally from the closely juxtaposed distal nodal bands of the erect axes; terminal fertile areas to 220–250 μ in diameter, resembling those of *Equisetum* in form.

Thallis 4–5 mm. altis e filamentis basilaribus repentibus a rhizoideis nodularibus affixis et ramis sparsis irregularibus erectis apicibus obtusis eforcipatis, axilaribus erectis 120–140 μ diametro, cortice interrupto, vittis corticosis nodi 1½–2-plo latioribus quam longis a circulo angusto centrali cellulis majoribus et

lateribus ambis corio cellulis minoribus anguloris ad 10 μ diametro, tetrasporangiis cruciatis ovatis ca. 40 μ longis in involucris valde inflatis eis ex vittis nodoris proxime juxtaposis axilarum erectarum acropetaliter productis, loculis fertilibus terminalibus 220–250 μ diametro eis *Equisetum* similantibus.

TYPE: Dawson 13620a, growing within tufts of *Ectocarpus breviarticulatus* near the margin of the seaward reef opposite EMBL, Parry Island, August 19.

This material is nearest to *Ceramium nakamurai* Dawson from Garanbi, Formosa (*C. equisetoides* Nakamura), but is not dichotomously branched. It is identical with tetrasporangial specimens cited and illustrated by the writer as a probable undescribed species from Isla San Benedicto, Mexico (Dawson 1954a: 6, pl. 4, fig. 2).

Ceramium gracillimum var. *byssoideum* (Harvey) G. Mazoyer; Dawson 1954: 448, fig. 55e, f; Dawson 1956: 53; Taylor 1950: 138 (as *Ceramium byssoideum* Harvey)
D. 13616, 13707, 13715, 13790, 13831, 13860, 13891, 13924, 13916, 13951, 14028.

Ceramium mazatlanense Dawson; Dawson 1954: 448, fig. 55g–j; Dawson 1956: 53
D. 13752, epiphytic on *Caulerpa*.

Ceramium serpens Setchell and Gardner ?; Dawson 1956: 54, fig. 53
D. 13610b, 13857. Both are sterile and not positively identified.

Ceramium taylori Dawson; Dawson 1954: 446, fig. 55b, c
D. 13637, epiphytic on *Udotea*, 13817, 13942.

Centroceras apiculatum Yamada; Dawson 1956: 55, fig. 55
D. 13941a, 14016.

Centroceras clavulatum (C. Agardh) Montagne; Dawson 1954: 446, fig. 54b; Dawson 1956: 55; Taylor 1950: 139
D. 13639, 13794, 13808, 13838, 13958 (this latter collection consists largely of f. *inerme* (Kützing) Piccone. P. 52–29, Aomon Is. shore rocks, 10/22/52.

Centroceras minimum Yamada; Dawson 1956: 54, fig. 54
D. 13640a, 14009a.

Spyridia filamentosa (Wulfen) Harvey; Dawson 1954: 444, fig. 54i, j; Dawson 1956: 56; Taylor 1950: 139
D. 13677, 13816, 13884, 13911. P. 1163, Mui Is. lagoon, 4/11/54; P. 1190, Bokanjoio Is. lagoon, 4/14/54.

Hypoglossum minimum Yamada 1936: 138, fig. 2A—D (Naha, Okinawa)

Fig. 30*c*

D. 13704, 13755, 13901, 13999d. These show considerable variation in form and habit. Those under 13999d, epiphytic on *Halimeda* from a depth of 135 feet, are most like Yamada's type.

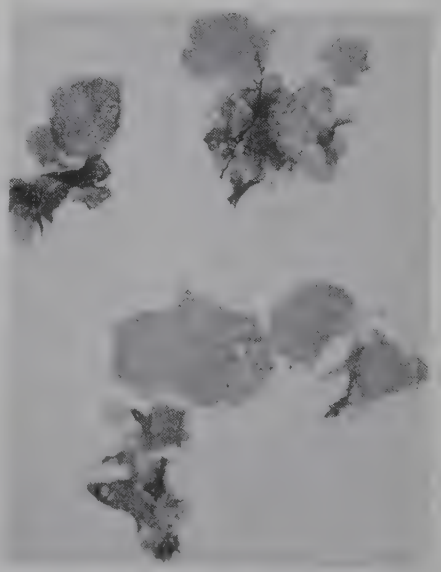


FIG. 28. *Hemitrema fragilis*: Habit of dry plants of D. 13801, × 1.3.

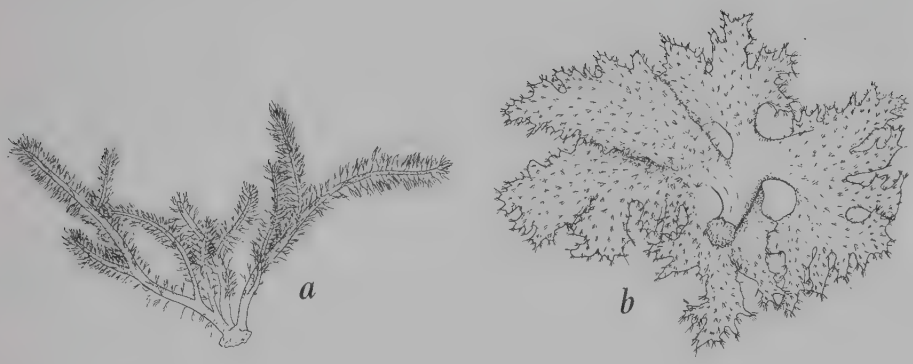


FIG. 29. *a*, *Dasya mollis*, prox.: Habit of a plant of D. 13876, × 4. *b*, *Dasyopsis geppii:* Habit of a young plant of D. 13728 as seen from below, × 3.5.

Taenioma perpusillum (J. Agardh) J. Agardh; Dawson 1954: 451, fig. 58a

D. 14035c. P. 2833a, 1½ mi. off Igurin Is. in the lagoon at 50 ft., 3/16/55.

Hemitrema fragilis (Harvey) comb. nov. *Martensia fragilis* Harvey 1954: 145 (Ceylon); Dawson 1956: 56, fig. 58

Fig. 28

D. 13737, 13801, 14008. Inasmuch as Silva (1952: 291) has pointed out that "*Hemitrema* seems to be the earliest available name for *Martensia*" which is illegitimate, this new combination is called for here.

Dictyurus purpurascens Bory; Dawson 1956: 57; Taylor 1950: 143, pl. 78, fig. 1

D. 13773. P. 2836, Parry Is. seaward reef edge near EMBL, 4/4/54.

Dasya iyengarii Børgesen 1937: 345, figs. 16, 17 (Pam ban Bridge, South India)

Fig. 22*b*

D. 13608, 13624, 13803, 13890, 14051. These specimens are somewhat variable in stature and in detail of branching, but seem to be essentially identical with the south Indian plant. The epiphytic specimens under D. 13608 are especially like the type. Saxicolous specimens under D. 13624 are provided with somewhat more attenuate and less curved and hooked penicilli, but appear otherwise to be like the epiphytic form. The best stands of the plant occur near the margin of the seaward reefs where the species may be dominant in some areas.

Dasya mollis Harvey, prox.; Harvey 1853: 62 (Key West, Florida); Taylor 1928: 173, pl. 26, fig. 13

Fig. 29*a*

D. 13876. This small, completely corticated plant seems best referred here, but the sterile material is insufficient for positive identification. It differs from Atlantic material mainly in the shorter cells of the ramelli.

Dasya adhaerens Yamada 1944: 43, pl. 7, fig. 1 (Ant Atoll, Caroline Islands); Taylor 1950: 141, pl. 79, fig. 1

T. 46–392. Not collected again.

Dasyopsis geppii Weber van Bosse 1913: 130, pl. 13, figs. 18–20, pl. 14, fig. 33 (reefs and to 20–25 fathoms at four Indian Ocean localities indicated)

Fig. 29*b*

D. 13728, 14007. Except for the more pronounced peltate form of some, these agree very well with the account of the "Sealark Expedition" material. Some of them show a

habit more like that of *Dasyopsis palmatifida* W. v B. from the same localities, and suggest further that it is only a variant of *D. geppii*.

Heterosiphonia wurdemannii var. *laxa* Børgesen; Dawson 1956: 57, fig. 60; Taylor 1950: 140 (as *H. wurdemanni*)
D. 13609, 13698, 13739, 13750, 13781, 13760, 13895, 13999. A common small species growing under a variety of conditions and showing variable habit but mostly tending toward Børgesen's var. *laxa*.

Polysiphonia coacta Tseng, prox.; Dawson 1954: 456, fig. 60g, h; Dawson 1956:57
D. 13857d, 13922.

Polysiphonia subtillissima Montagne; Dawson 1954: 454, fig. 60c; Dawson 1956: 58
D. 13904.

Polysiphonia tongatensis Harvey; Dawson 1954: 454, fig. 60d, e; Dawson 1956: 57
D. 13644, 13906, 13933, 13925, 13950c.

Tolypiocladia calodictyon (Harvey) Silva; Dawson 1956: 58, fig. 62; Taylor 1950: 148, pl. 57, fig. 2 (as *Rochera calodictyon*)
D. 13625, 13705, 13881, 13834, 13899, 13957. P. 18129, Runo Is. lagoon at 60 ft., 3/8/55; P. 2500, ¼ mi. off Engebi Is. in lagoon at 15 ft., 3/2/55; P. 2816, s.e. end of Bokanjoio Is. in lagoon at 60 ft., 3/8/55; P. 22x, Runit Is. n.w. tip on channel, 10/22/52; P. 60, off n. tip of Igurin Is. in lagoon at 20 ft., 10/28/52; P. 1153, Engebi Is. lagoon, 4/11/54.

Herposiphonia secunda (C. Agardh) Ambronn; Dawson 1956: 58, fig. 63; Taylor 1950: 148
D. 14002a, growing on the membrane of *Valonia ventricosa*.

Herposiphonia tenella (C. Agardh) Ambronn; Dawson 1954: 452, fig. 59a; Taylor 1950: 147; Dawson 1956: 59
D. 13771a, 13904a, 13914, 14017.

Lophosiphonia bermudensis Collins and Hervey; Dawson 1956: 59, fig. 65
D. 13696, 13903a, 13999a, 14035b. My attention has been called to the fact that Howe (1918: 521) has reduced this species under *Dipterosiphonia rigens* (Schousb.) Falkenb. It appears that a more critical review is called for than can be attempted here.

Lophosiphonia obscura (C. Agardh) Falkenberg; Dawson 1954: 451, fig. 58d, e
D. 13648, 13867. The latter is virtually identical with Børgesen's 1918 figure of tetrasporic material.

Laurencia mariannensis Yamada; Dawson 1956: 60, fig. 66; Taylor 1950: 144, pl. 55, fig. 1
D. 13747. P. 2587a, Aitsu Is., 2/11/55; P. 2832, Igurin Is. lagoon at 50 ft., 3/16/55.

Laurencia nana Howe 1920: 566 (Mariguana, Bahamas)

Fig. 30*a*

D. 13725. These fertile specimens are in excellent agreement with Howe's description, including the palisade cortical cells, the presence of rhizoidal haptera and the lack of lenticular thickenings.

Laurencia parvipapillata Tseng; Dawson 1954: 458, fig. 61g
D. 13754, 13964. P. 2833, Igurin Is. lagoon at 50 ft., 3/16/55.

Chondria minutula Weber van Bosse 1923: 349, pl. 10, figs. 10, 12 (Tanah Djampea Is., Indonesia)

Fig. 30*d*, *e*

D. 13744, 13771, 13932a, 13788a. The tetrasporic and cystocarpic material seems to agree well with Weber van Bosse's account of the type which had a similar creeping habit and the same stature.

Chondria polyrhiza Collins and Hervey 1917: 121, pl. 2, fig. 12 (Bermuda)

Fig. 30*b*

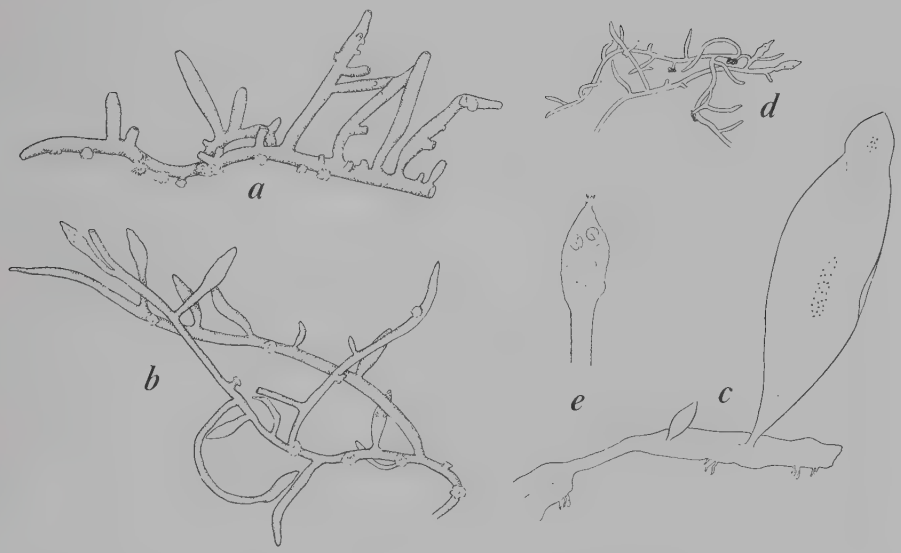


FIG. 30. *a*, *Laurencia nana:* Habit of a plant of D. 13725, × 4. *b*, *Chondria polyrhiza:* Habit of a plant of D. 13795 from the under side, × 10. *c*, *Hypoglossum minimum:* Part of a tetrasporangial plant of D. 13704 showing rhizoids, branching from the midrib, and a sorus, × 6. *d*, *e*, *Chondria minutula: d*, Habit of a plant of D. 13744, × 5; *e*, detail of the apex of a tetrasporic branch of the same showing the emergent tip and trichoblasts, × 35.

D. 13795. This seems to fit the Collins and Hervey description and figures well. Under D. 14027 two forms are present, one with axes to 450 μ in diameter and with rather blunt tips, the other with axes only about 220 μ in diameter and more attenuate tips. They probably represent growth stages.

Chondria repens Børgesen; Dawson 1954: 460, fig. 62d, e; Dawson 1956: 60
D. 13932.

BLUE-GREEN ALGAE

Anacystis dimidiata (Kützing) Drouet and Daily 1952: 221. *Trochiscia dimidiata* Kützing 1833: 593, fig. 75 (Germany). Taylor 1950: 103 (as *Gloeocapsa turgida* (Kütz.) Hollerbach [*Chroococcus turgidus* (Kütz.) Nägeli])

Fig. 31*a*

P. 2830, Igurin Is. scum on rocks in lagoon at 50 ft., 3/16/55.

Coccochloris stagnina Sprengel 1807: 14 (Halle, Germany)

Fig. 31*b*

D. 13893, 14043. P. 1235–6, Bogombogo Is. lagoon, 4/22/54; P. 2801, Bokanjoio Is. seaward flats. 10/25/54.

Gomphosphaeria aponina Kützing 1836: Dec. 16, no. 151 (Abano, Italy); Taylor 1950: 103

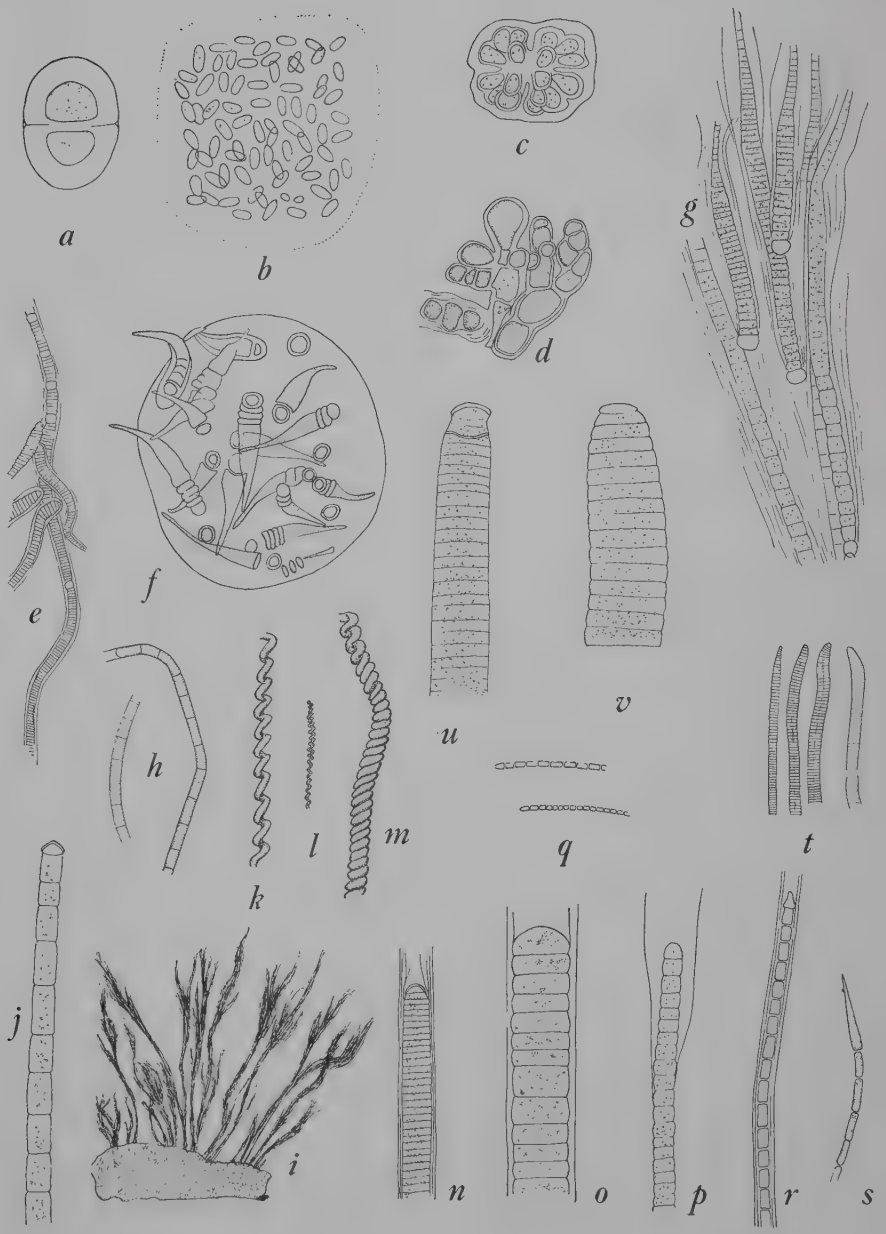
Fig. 31*c*

T. 46–316. Not collected again.

Entophysalis conferta (Kützing) Drouet and Daily; Dawson 1954: 379, fig. 3r
D. 13664.

Entophysalis deusta (Meneghini) Drouet and Daily 1948: 79. *Coccochloris deusta* Meneghini 1841: 173 (Genoa, Italy). Taylor 1950: 104 (as *E. granulosa* Kütz.)

Fig. 31*d*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D. 13673, 13878b.

Hormothamnion enteromorphoides Grunow seq. Bornet and Flahault; Dawson 1954: 379, fig. 3n; Taylor 1950: 105
D. 13680, 13682. P. 22, Rigili Is., 8/10/49.

Plectonema nostocorum Bornet seq. Gomont 1893: 102, pl. 1, fig. 11 (type not indicated); Taylor 1950: 105.
T. 46–304. Not collected again.

Plectonema terebrans Bornet and Flahault seq. Gomont 1893: 103 (Le Croisic, Atlantic France)

D. 13878a, 14020. P. 2830, Igurin Is. lagoon rocks at 50 ft., 3/16/55.

Scytonema polycystum Bornet and Flahault 1887: 90 (Noumea, New Caledonia)
D. 13955.

Scytonema myochrous (Dillwyn) C. Agardh seq. Bornet and Flahault is reported by Palumbo 1950 from Eniwetok without locality, based upon a determination by F. Drouet.

Calothrix crustacea Thuret seq. Bornet and Flahault 1886: 359 (Le Croisic, Atlantic France)

Fig. 31*e*

D. 13621, 13662, 13687, 13868.

Rivularia atra Roth seq. Bornet and Flahault 1886: 353 (Europe)

Fig. 31*f*

D. 13663.

Rivularia polyotis (J. Agardh) seq. Bornet and Flahault 1886: 360 (Mediterranean Sea)

Fig. 31*g*

D. 14034.

Phormidium crosbyanum Tilden 1910: 96, pl. 4, figs. 60, 61 (Waianae, Oahu, Hawaiian Islands); Taylor 1950: 109

Fig. 31*h*

D. 13670, 13880, 14052. P. 2800, Mui Is. seaward flats, 10/21/54; P. 2841, Eneroul Is. seaward flats, 9/23/54; P. 2818, Bokanjoio Is. sand flats on east side, 3/8/55.

Phormidium penicillatum Gomont 1893: CLIX, pl. IV, figs. 5–7 (Borbon Is., Mascarene Islands)

Fig. 31*i*, *j*

D. 13714, 13780, 13963.

Oscillatoria nigro-viridis Harvey seq. Gomont; Dawson 1954: 380, fig. 3g
D. 13686.

Spirulina major Kützing seq. Gomont 1893: 251, pl. 7, fig. 29 (Germany)

Fig. 31*k*

D. 13885.

Spirulina subsalsa Oersted seq. Gomont 1893: 253, pl. 7, fig. 32 (Denmark)

Fig. 31*m*

D. 13662a, 13846.

◄ FIG. 31. *a*, *Anacystis dimidiata:* × 600 approx. (after West). *b*, *Coccochloris stagnina:* × 600 approx. (after Lemmermann). *c*, *Gomphosphaeria aponina:* × 600 approx. (after West). *d*, *Entophysalis deusta:* × 600 approx. (after (Engler and Prantl). *e*, *Calothrix crustacea:* × 500 approx. (after Bornet and Thuret). *f*, *Rivularia atra:* × 600 approx. (after Wille). *g*, *Rivularia polyotis:* × 600 approx. (after Bornet and Thuret). *h*, *Phormidium crosbyanum:* × 600 approx. (after Tilden). *i*, *j*, *Phormidium penicillatum: i*, Habit, × 0.8; *j*, detail of a trichome, × 580 (after Bornet). *k*, *Spirulina major:* × 600 approx. (after Gomont). *l*, *Spirulina tenerrima:* × 600 approx. *m*, *Spirulina subsalsa:* × 600 approx. (after Gomont). *n*, *Lyngbya semiplena:* × 600 approx. (after Gomont). *o*, *Lyngbya sordida:* × 600 approx. (after Gomont). *p*, *Lyngbya gracilis:* × 600 approx. (after Gomont). *q*, *Schizothrix lacustris:* × 600 approx. (after Gomont). *r*, *Symploca laeteviridis:* × 600 approx. (after Gomont). *s*, *Microcoleus tenerrimus:* × 600 approx. (after Gomont). *t*, *Hydrocoleum glutinosum:* × 600 approx. (after Kützing). *u*, *Hydrocoleum comoides:* × 600 approx. (after Gomont). *v*, *Hydrocoleum cantharidosmum:* × 600 approx. (after Gomont).

Spirulina tenerrima Kützing seq. Gomont 1893: 252 (Europe)

Fig. 31*l*

D. 13799, 13970.

Lyngbya aestuari (Mertens) Liebmann seq. Gomont; Dawson 1954: 380, fig. 3a; Taylor 1950: 110
D. 13659, 13684, 13855, 13878, 13984.

Lyngbya confervoides C. Agardh seq. Gomont; Dawson 1954: 380, fig. 3b, c; Taylor 1950: 110
D. 13940, 14038.

Lyngbya majuscula (Dillwyn) Harvey seq. Gomont; Dawson 1954: 380, fig. 3d; Taylor 1950: 111
D. 13646, 13690, 13784, 13844, 13848, 13882, 13960, 13965, 13985. P. 2853, Rigili Is. sea beach, 11/17/54; P. 14, Engebi Is. n.w. end at 6 ft., 8/11/49; P. 2828, Igurin Is. 1½ mi. off at 50 ft., 3/8/55.

Lyngbya meneghiniana (Kützing) seq. Gomont 1893: 125 (Europe); Taylor 1950: 109
D. 13681, 13683, 13885a, 13984a.

Lyngbya semiplena (C. Agardh) J. Agardh seq. Gomont 1893: 138, pl. 3, figs. 7–11 (Adriatic Sea)

Fig. 31*n*

D. 13686a, 14041. P. 57b, Rigili Is. seaward pavement, 10/27/52.

Lyngbya sordida (Zanardini) seq. Gomont 1893: 126, pl. 2, fig. 21 (Venice, Italy); Taylor 1950: 110, pl. 79, fig. 2

Fig. 31*o*

D. 13789, 13931, 13966, 14030. P. 52–18, Runit Is. flats at w. tip, 10/22/52. P. 52–104, Aaraanbiru Is. lagoon s.w. end, 11/7/52.

Lyngbya sordida f. *bostrychicola* Crouan seq. Gomont 1893: 126 (near Brest, France)
D. 13783.

Lyngbya gracilis (Meneghini) Rabenhorst seq. Gomont 1893: 124, pl. 2, fig. 20 (Atlantic France); Taylor 1950: 109

Fig. 31*p*

T. 46–421. Not collected again.

Schizothrix lacustris A. Braun seq. Gomont 1892: 301, pl. 6, figs. 9–12 (Germany); Taylor 1950: 112

Fig. 31*q*

T. 46–333, Runit Is. seaward reef flat, May 1946. Not collected again.

Symploca hydnoides Kützing seq. Gomont; Dawson 1954: 380, fig. 3o, p
D. 13641, 13689, 13839, 13993, 14042. P. 2839, Runit Is. n.w. tip flats in channel, 10/22/52; P. 2809, Bokanjoio Is. lagoon, 3/8/55; P. 2838, Mui Is. lagoon, 4/11/54; P. 1151, Runit Is. n. tip channel, 4/11/54; P. 2843, Bogombogo Is. seaward flats, 10/5/54.

Symploca laete-viridis Gomont 1893: 109, pl. 2, figs. 6–8 (Key West, Florida); Taylor 1950: 113

Fig. 31*r*

D. 13833.

Microcoleus tenerrimus Gomont 1892: 355, pl. 14, figs. 9–11 (France)

Fig. 31*s*

D. 13659a, 13872.

Hydrocoleum coccineum Gomont 1892: 342, pl. 13, figs. 1, 2 (on *Codium* Antibes, Mediterranean Sea); Taylor 1950: 115
D. 13779. This species is similar to *H. lyngbyaceum* but differs in its red to pale blue-green protoplasm (bright blue-green, olive

or yellow green in *H. lyngbyaceum*). In the latter the cross walls are granulated unlike *H. coccineum*.

Hydrocoleum glutinosum (C. Agardh) Gomont 1892: 339 (Sweden)

Fig. 31*t*

D. 13661, 13668, 13756, 13842.

Hydrocoleum comoides (Harvey) seq. Gomont 1892: 335, pl. 12, figs. 3–5 (Australia); Taylor 1950: 115

Fig. 31*u*

D. 13638, 13685, 13688, 13716, 13733.

Hydrocoleum lyngbyaceum Kützing seq. Gomont; Dawson 1954: 380, fig. 3q

D. 13653, 13667, 13671, 13827, 13870. P. 2543, Runo Is. seaward reef, 3/8/55; P. 2802, Bokanjoio Is. seaward flats, 10/25/54; P. 2810, Bokanjoio Is. lagoon, 3/8/55; P. 2823, Bokanjoio Is. seaward reef, 3/8/55; P. 2852, Mui Is. lagoon, 11/17/54; P. 2856, Aitsu Is. lagoon, 11/17/54.

Hydrocoleum cantharidosmum (Montagne) seq. Gomont 1892: 336, pl. 12, figs. 6, 7 (Canary Islands); Taylor 1950: 116

Fig. 31*v*

T. 46–312. Not collected again.

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part II. Collection from Arno Atoll, Marshall Islands[1]

ALBERT H. BANNER[2]

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Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean
Part II. Collection from Arno Atoll, Marshall Islands[1]

Albert H. Banner[2]

This paper reports upon a collection of snapping shrimp made by Dr. Robert W. Hiatt and Dr. Donald W. Strasburg, of the University of Hawaii, at Arno Atoll in the southern portion of the Radak chain of the Marshall Islands. Under the sponsorship of the Pacific Science Board with funds from the Office of Naval Research, they visited Arno during the summer of 1950 as a part of a scientific team to investigate the total ecology of the atoll. One additional shrimp reported upon was collected by Dr. J. W. Wells of the same investigation.

This study of the snapping shrimp from Arno was initiated under a grant administered by the U. S. National Museum and the Pacific Science Board under a contract between the Office of Naval Research, Biology Branch, and the National Academy of Sciences, (NR 160–175); some help in the final phases of the study was made available through a grant to the author from the National Science Foundation (NSF-G-1754).

To avoid repititious synonymies and bibliographies in this series of papers, whenever a full citation for a species has been given in an earlier paper, by myself, reference is made to this citation. In this present paper reference is made only to Part I of these studies, describing collections from the Mariana Archipelago (Banner, 1956). Type specimens for the new species described in this paper will be deposited in the United States National Museum.

Arno Atoll

The nature and biology of Arno Atoll has been covered in a series of preliminary reports by members of the investigation team, published (in mimeographed form) in the *Atoll Research Bulletin* (issued by the Pacific Science Board), Numbers 3–11, 1951–1952. A comprehensive book on these studies is now in preparation and specialized scientific reports are appearing in technical journals.

Arno is an irregularly shaped atoll centered about 7° 05′ N., 17° 40′ E. and about 27 miles across its longest axis (Fig. 1). It consists of 133 islands and islets, only a few of which are large enough to support human habitation. The outer margin of the atoll drops off steeply into waters of profound depth; within, the lagoon is estimated to be 100–200 feet deep. The ocean communicates with the lagoon through a series of passes, deep or shallow. The atoll lies in the belt of northeasterly trades and at the southern edge of the North Equatorial Current, which may be replaced during some of the months of northern summer by the Equatorial Countercurrent. The ring of islands is surrounded on both inner and outer margins by coral reefs of varying vitality and breadth, depending upon conditions of wind, surf, sediment, etc.

[1] Contribution No. 89, Hawaii Marine Laboratory.

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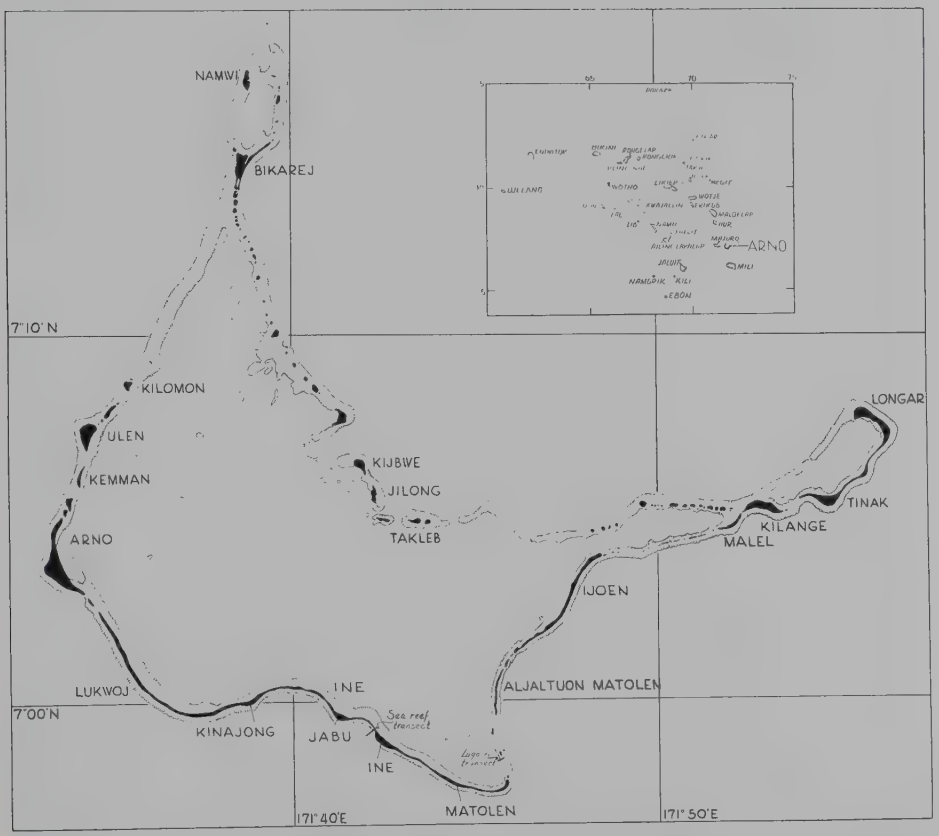

FIG. 1. Map of Arno Atoll, showing collecting stations. *Insert*: A map of the Marshall Islands, showing the location of Arno.

HABITATS OF THE SHRIMP

The studies made by Dr. Hiatt include two ecological sections of the reef in the extreme southern section of the atoll, one on the seaward and one on the lagoon side. The study of the seaward reef was made near the village of Ine, in a region quite protected from the prevailing winds and surf; that of the lagoon reef was made off the islet of Makïn, some 4 miles away.

The method of taking the transects was the same in both cases. A strip 50 feet wide and divided into sections, 50 feet long on the seaward reef and 100 feet long on the lagoon reef, was laid out normal to the shore and running from the beach to water beyond "skin diving" depth. The animals in each section were collected, given field identification and preserved; in the shallow zones this was done by wading, in the deeper by "skin diving."

The contours found on both transects were about the same, showing a broad, relatively flat, gradually sloping reef centering about the height of mean low water. An abrupt change in slope marked the outer margins of the reef flat, with the slope becoming steep on the lagoon reef and precipitous on the ocean side.

A complete report on the ecological study is in preparation by Dr. Hiatt. For this report on a small section of his collections, loaned to me for this study, Dr. Hiatt has permitted me to extract and summarize the following information from his field notes about the zones and specific habitats of the shrimp:

E–1–2. Section XI, seaward reef. Slope beyond edge of reef flat, about 450 feet from shore. Reef face at an angle of about 60°. 82 species of coral collected down to depth of 30 feet, no species being dominant. Alpheids commensal with *Antedon*, a sea lily found clinging to the underside of coral ledges.

E–1–106. Section III, seaward reef. 50–100 feet from beach. Level about that of mean low water (0.0); on low tides area with dry areas and shallow pools. Corals not flourishing, *Montipora gaimardi* the dominant species. Sand and coral fragments in depressions. Alpheids in interstices of *M. gaimardi*.

E–1–122. Section IV, seaward reef. 100–150 feet from beach. In general similar to Section III, about same level. Alpheids as in Section III.

E–1–149. Section V, seaward reef. 150–200 feet from beach. Inner portion alone exposed on extreme low water, outer portions covered by 2–5 inches of water. Level of extreme low water marks division between *M. gaimardi* and *Acropora pectinata* zones. Alpheids as in Section III.

E–1–285, 290. Section VI, seaward reef. 200–250 feet from beach. Water standing at all tides, reef flat bare with no loose sand. Zone with mixed *M. gaimardi* and *A. pectinata*. Alpheids in group 285 collected from living heads of coral and in holes in dead coral, and in group 290 from living heads of *Pocillopora*.

E–1–305. Collected from a brackish pond on Malel Island.

E–1–306. Section VII, seaward reef. 250–300 feet from shore. At tides below 0.3, tips of growing heads of coral exposed. *A. pectinata* dominant coral, covering much of area; *Pocillopora* luxuriant. Alpheids from dead bases and living branches of coral; some from living heads of *Pocillopora*.

E–1–387, 388. Section VIII, seaward reef. 300–350 feet from shore. Highest parts of corals exposed only on extreme low waters. *A. pectinata* dominant with *Pocillopora* secondary; a brown alcyonarian, *Lobularia krempfi*, also occurring in numbers. Alpheids collected from heads of *Acropora* and *Pocillopora*.

E–1–611, 630, 643, 648. Section IX, seaward reef. 350–400 feet from shore. Section similar to Section VIII, the depth slightly greater and area commonly flooded with foam from surf much of day. *A. pectinata* and *Pocillopora* still dominant corals. Alpheids collected from heads of *Acropora* (617,643), *Pocillopora* (619, 630), and *Stylophora* (648).

E–1–670. Section II, seaward reef. From edge of water at mean high tide to a point 80 feet seaward. Exposed beachrock pitted and covered with fine, short algae; area marked by large tide pools varying from 4 to 8 inches deep. Alpheids collected from tide pool.

E–2–169, 311. Section II, lagoon reef. From mean high tide level to 100 feet towards the lagoon. Outer margin uncovers at 0.0 tide. Covered with quite smooth beachrock, with a few shallow tide pools; outer portions covered by a fine sand veneer. No corals present. Alpheids collected under loose slabs of beachrock (169) and in holes in the rock (311).

E–2–343, 382. Section IV, lagoon reef. From 200–300 feet from shore, depth from 4 to approximately 60 feet. Area with bottom covered with sand and coral rubble, and numerous species of coral with those of the genus *Acropora* dominant. Alpheids collected from heads of *Seriatopora hystrix* (343) and *Stylophora* (382).

E–2–360. Section III, lagoon reef. From 100–200 feet from shore. Depth from 0.0 to 4 feet. Section of bottom covered with fine sand and coral rubble; luxuriant growth of corals with species of *Acropora* dominant. Alpheids collected from *Stylophora mordax*.

ATHANAS Leach

Athanas djiboutensis Coutière, 1897

For synonymy, see Banner, 1956.

LOCALITIES: One specimen each at E–1–290 and E–1–388.

DISCUSSION: The two specimens cannot be assigned positively to this species for they are both fragmentary, lacking their chela and some other appendages. However, the appendages still remaining, and especially the form of the rostrum and the orbital spines about the eyes, compare almost perfectly with the specimens from Saipan identified as this species.

Athanas marshallensis Chace
Fig. 2

Athanas marshallensis Chace, U. S. Natl. Mus., Proc. 105(3349): 17, fig. 8, 1955.

LOCALITIES: One non-ovigerous female from E–1–122.

DISCUSSION: This specimen differs in only one way from the description and figure of Chace: in this specimen the extracorneal spines reach almost to the anterior margin of the eyes, instead of midway along the eyes as in Chace's specimens. It is likely, however, that the eyes are rotated backwards towards the body, for the "collar" of the anterior carapace that usually fits snugly about the eyes is loose and stands out from the corneas in this specimen.

METABETAEUS Borradaile

Metabetaeus minutus (Whitelegge)

Betaeus minutus Whitelegge, Austral. Mus., Mem. 3: 147, pl. 7, fig. 4, 1897.

Metabetaeus minutus Borradaile, Zool. Soc. London, Proc. 66: 1014, 1898.

Metabetaeus minutus Coutière, Soc. Ent. de France, Bul. 1899(19): 374, 1899a.

LOCALITIES: Four specimens, all females without eggs, maximum length 17 mm., E–1–305.

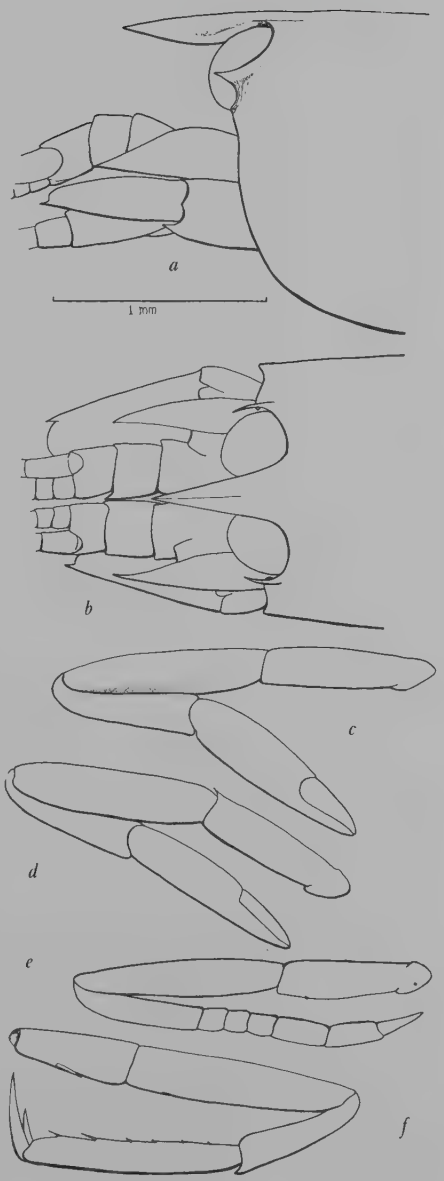

FIG. 2. *Athanas marshallensis* Chace. *a*, *b*, Anterior body region; *c*, right cheliped; *d*, left cheliped; *e*, second leg; *f*, third leg. (All same scale.)

DISCUSSION: These specimens agree almost perfectly with Whitelegge's original description and with the later redescriptions. The only differences found are in the anterior body region when compared to the plate of the original description. In these specimens the rostrum is almost an equilateral triangle with straight sides and slightly rounded tip, while Whitelegge showed and described his specimen as having a slightly more narrow rostrum with concave sides and an acute tip. Further, the concavity between the base of the rostrum and the orbital spines is more pronounced. Finally a difference is found on the relative lengths of the antennular and antennal peduncles, for in these specimens the antennular peduncle is slightly longer than the antennal, rather than the reverse as described by Whitelegge. These differences are minor and most likely of no importance.

Otherwise the specimens agree in the general form, the proportions of the appendages, the branchial formula and even in the possession of a brown spot on *corpus mandibulae* described by Coutière.

The type specimens came from a mangrove swamp, and, previous to this report, were the only specimens known. The ones described from Arno came from a brackish pond.

SYNALPHEUS Spence Bate

Comatularum Group

Synalpheus carinatus (de Man)

Alpheus carinatus de Man, Arch. f. Naturgesch., 53: 508, pl. 22, fig. 2, 1887.

Synalpheus carinatus de Man, Siboga Exped. 39a¹(2): 210, pl. 5, fig. 23, 1911.

nec Synalpheus carinatus Pearson, Report on Pearl Oyster Fisheries, p. 83, pl. 2, fig. 9, 1905.

LOCALITIES: One specimen at E–1–2, (commensal with *Antedon*, a sea lily).

DISCUSSION: This specimen agrees perfectly with the characteristics given by de Man. The ova are 1.1 by 0.7 mm. The species will be discussed more fully in a later paper. Hiatt notes that the color in life was brownish-black, the same as the host, *Antedon*.

Synalpheus consobrinus de Man

Synalpheus consobrinus de Man, Nederland. Dierk. Ver., Tijdschr. II, 11: 111, 1909.

Synalpheus consobrinus de Man, Siboga Exped., 39a¹(2): 204, pl. 6, fig. 21, 1911.

LOCALITIES: One specimen at E–1–643.

Neomeris Group

Synalpheus charon charon (Heller)
Fig. 3

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens each at E–1–617 and E–1–630.

DISCUSSION: These four specimens are of the parent subspecies with the expanded base to the superior unguis of the third to fifth legs, and with a rostrum of uniform taper.

One specimen from E–1–617, however, had a greatly expanded palm of the large chela with greatly reduced fingers. The condition is slightly more pronounced than that found in *S. macromanus* Edmondson (1925: 9), and at first the specimen was tentatively identified as that species. But *S. macromanus* has a conical inferior unguis on the third leg and is otherwise similar to *S. paraneomeris* Coutière, while this specimen is identical to *S. charon* except for the form of the large and small chelae.

The question is how this enlargement of the chela should be interpreted. When there was but the one specimen known as *S. macromanus* it was logical to consider the modification to be of specific worth; if this specimen were similar to *S. macromanus*, that species would have been considered as more valid. However, with specimens related to two different species showing a parallel mutation, I believe that the condition could best be interpreted as a growth anomaly that may occur in several species of this genus. The fact that this spec-

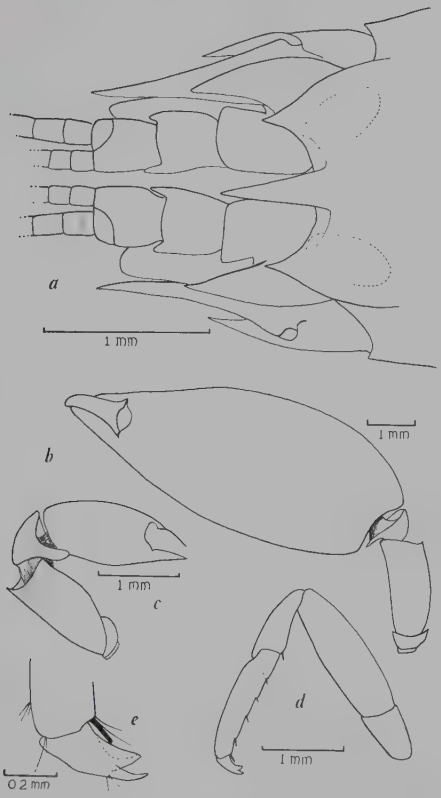

FIG. 3. *Synalpheus charon charon* Banner, aberrant form. *a*, Anterior body region; *b*, inflated large chela and cheliped; *c*, small cheliped of normal form; *d*, third leg; *e*, third leg, dactylus.

imen was one of a sole pair, male and female, the other being plainly *S. charon charon*, collected at one locality would offer support to this conclusion.

If this be so, then the original *S. macromanus* must be considered to be an aberrant form of *S. paraneomeris* Coutière.

Synalpheus paraneomeris Coutière

For synonymy, see Banner, 1956.

LOCALITIES: One specimen at E–1–106, 3 at E–1–306.

Coutierei Group

Synalpheus coutierei Banner

Fig. 4

Synalpheus coutierei Banner, Pacific Sci. 7(1): 36, 1953.

Synalpheus biunguiculatus Coutière, Soc. Ent. de France, Bul. 1898(11): 232, figs. 1–4, 1898 [and other authors—see Banner *op. cit.*].

nec Alpheus biunguiculatus Stimpson, Acad. Nat. Sci. Phila., Proc. 1860: 31.

LOCALITY: Three specimens at E–2–382.

DISCUSSION: These specimens are plainly of this species as illustrated by Coutière (*loc. cit.* and 1905: 873, pl. 31, fig. 8). However, they show slight differences in the proportions of the various parts of taxonomic significance, most apparently in the antennular peduncle, wherein the second article is relatively longer, in the small cheliped, in the dactylus of the third leg, and in the telson. These variations are shown in Figure 4.

Coutière (1898) has shown some variations in the anterior regions and in the dactyli of specimens collected in various parts of the Indian Ocean which approach the differences noted here; he also (1905: figs. 8, 10) described and depicted the form found in the Maldive and Laccadives, and described as a separate variety a form whose variations markedly exceed those of this group of specimens. I believe that considering the variations already reported and the variations in related species of *Synalpheus*, no taxonomic importance should be attached to the slight differences found in these specimens from Arno.

Synalpheus lophodactylus Coutière

Synalpheus lophodactylus Coutière, Soc. Philomath. Paris, Bul. IX, 11(5): 7, 1908.

Synalpheus lophodactylus Coutière, Linn. Soc. London, Trans., Zool. II 17(4): 421, pl. 61, fig. 11, 1921. [Text the same as 1908 reference, plates not previously published.]

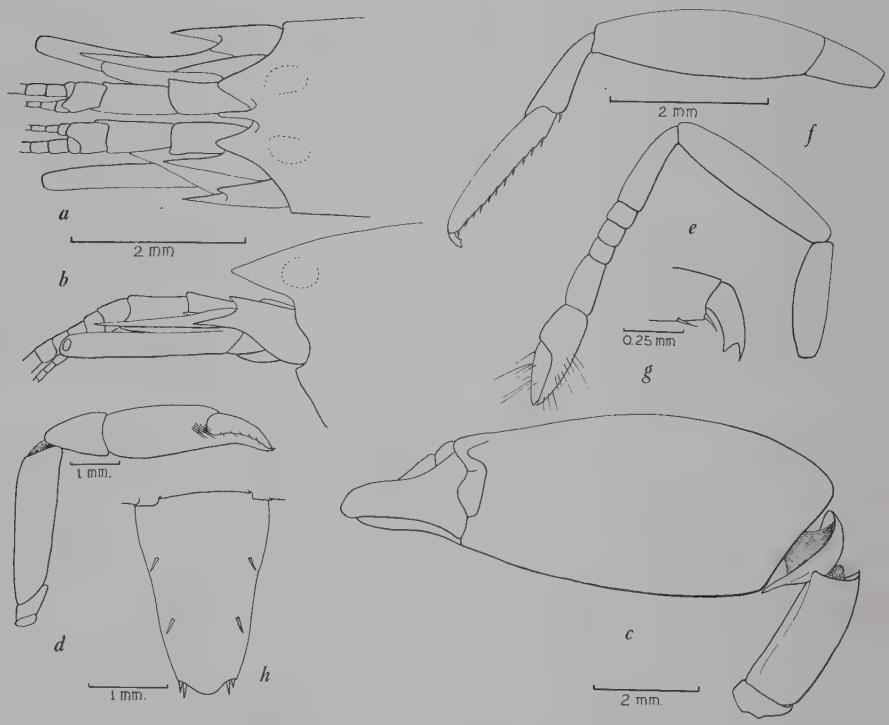

FIG. 4. *Synalpheus coutierei* Banner. *a*, *b*, Anterior body region; *c*, large cheliped; *d*, small cheliped; *e*, second leg; *f*, third leg; *g*, third leg, dactylus; *h*, telson.

LOCALITY: One female, collected at station E–2–343.

DISCUSSION: This specimen agrees well with Coutière's description and figures of his type, the sole specimen reported until now, except for several minor details. The setae on the small chela, shown as a definite tuft and described as "une brosse de soies sériées . . . moins sériées et moins abondantes que dans le groupe *laevimanus* . . .", appear to be less abundant in the distal tuft in this specimen and are also found proximal to the tuft in a row leading towards the articulation. The inferior distal margin of the merus of the third leg bear a feeble movable spine, instead of being unarmed as depicted by Coutière. Finally, the posterior lateral angles of the telson are produced into slender acute teeth almost as long as the lateral distal spines instead of being broader and relatively shorter as shown by Coutière. However, the proportions of the small chela and third legs are almost exactly the same as in the type.

The specimen described by Coutière lacked the large chela, which is intact but slightly distorted in this specimen. It is of typical form for the genus, with the fingers occupying the distal 0.3 of the chela, and the height being about 0.4 of the total length (this proportion may not be accurate because of the condition of the appendage). The merus is 0.5 as long as the chela and 2.5 times as long as broad. The merus and the dactylar articulation are unarmed.

ALPHEUS Fabricius

Megacheles Group

Alpheus deuteropus Hilgendorf, 1878

For synonymy, see Banner, 1956.

LOCALITY: One specimen at E–1–387.

Alpheus collumianus probabalis Banner, 1956

For synonymy of these subspecies and the parent species, see Banner, 1956.

LOCALITY: One specimen from the coral reef at Ine, collected by Wells.

DISCUSSION: The single specimen of this subspecies is markedly more hairy than were the specimens from Saipan; the long setae are especially noticeable on the antennular peduncle, the chelae, and the third and following legs. Moreover, the meri of the third and fourth legs bear 5–6 spines, instead of 4 as in the type, while the merus of the large chela has only 2 small weak spines instead of 6 strong spines that were carried by the type.

Alpheus collumianus medius Banner, 1956

LOCALITIES: Two specimens at E–1–387, 1 at E–1–617.

Macrochirus Group

Alpheus gracilis var. **simplex** Banner, 1953

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–306, both defective; 1 at E–1–387.

DISCUSSION: This single intact specimen is almost identical to the specimens from Hawaii except that it bears a trace of a rostral carina, a condition also noted in one of the aberrant specimens from Hawaii. The external spine of the uropod is black.

The two other specimens are assigned to this species with question for they are lacking their chelae and some of the other appendages. The parts remaining, as well as the structure of the anterior carapace, agree very well with the specimens from Hawaii.

Alpheus ventrosus Milne-Edwards, 1837

For earlier synonymy, see Banner, 1956.

Alpheus sp. Coutière, in Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 882, pl. 74, fig. 19, 1905.

Crangon latipes Banner, Pacific Sci. 7(1): 82, fig. 27, 1953.

LOCALITIES: Four specimens at E–1–290; 3 at E–1–306; 2 at E–1–387; 3 at E–1–617; 5 at E–1–630; 1 at E–2–343.

DISCUSSION: Specimens from station E–1–630 and E–1–290 present an incomplete intergradation from the form described as *C. latipes* and the mature *A. ventrosus*. The intergradation indicated by these specimens is confirmed by specimens from other areas and will be discussed more fully in a subsequent paper. One specimen in this collection shows the darkened spine on the uropods (as discussed in the specimens from Saipan).

Alpheus amirantei Coutière

Alpheus amirantei Coutière, Soc. Philomath. Paris, Bul. IX, 11(5): 15, 1908.

Alpheus amirantei Coutière, Linn. Soc. London, Trans., Zool. II, 17(4): 421, pl. 63, fig. 16, 1921. [Text the same as 1908 reference.]

LOCALITY: One specimen at E–1–611.

DISCUSSION: This specimen appears to be somewhat intermediate in many characters between the type that Coutière described for the Indian Ocean and the Hawaiian form. The relative lengths of the antennular peduncle, antennal peduncle and scaphocerite are subequal, like Coutière's specimen, instead of having the scaphocerite markedly the longest. The basicerite bears a relatively strong spine, like the Hawaiian specimen. This specimen, a female, has slightly longer fingers to the large chela than does the Hawaiian form. The second carpal article of the second leg is 2.7

times the length of the first, instead of 2.3 in the Hawaiian form, and 3.0 in Coutière's. The inferior distal tooth of the merus of the third leg is longer and more acute than in the Hawaiian form, therefore more like the type specimen. Finally, the Arno specimen is unlike both previous forms in the armature of the merus of the large and small chela. In Coutière's specimen the inferior internal margin of the merus carried a series of rounded serrations terminating in a strong acute tooth; in the Hawaiian specimens the serrations were lacking, and the tooth was weaker; in the Arno specimen the tooth also is lacking. The merus of the small chela was armed with a tooth in the type but in both the Hawaiian and Arno specimens the tooth is lacking.

However, as the specimen agrees well with the general description of *A. amirantei*, these differences are considered to be at most subspecific, and are more likely to be individual variation.

Alpheus nanus (Banner) 1953

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–306.

DISCUSSION: Like the specimens from Saipan, the sole specimen with the chelae intact, a male, had spinules on the inferior internal margin of the merus; both large and small chelae had seven such spinules. The other specimen, a female, was lacking in both chelae.

Alpheus paragracilis Coutière, 1897

For synonymy, see Banner, 1956.

LOCALITIES: One specimen at E–1–106; 2 at E–1–285; 3 at E–1–387; 2 at E–1–617.

Alpheus macrochirus Richters

Alpheus macrochirus Richters, Meeresfauna der Insel Mauritius und der Seychellen, Decapoda, p. 164, pl. 17, figs. 31–33, 1880.

nec Alpheus macrochirus de Man, Arch. f. Naturgesch. 53(1): 519, 1887.

LOCALITIES: Two specimens at E–1–306; 2 at E–2–360.

DISCUSSION: These specimens agree well with the short original description, with the characteristics given in de Man's key and discussion (1911) and with the three figures in Coutière's *Les Alpheidae* (1899, figs. 51, 52, 261).

Crinitus Group

Obesomanus Subgroup

Alpheus lutini Coutière, 1905

For synonymy, see Banner, 1956.

LOCALITIES: Three specimens at E–1–106; 12 at E–1–122; 30 at E–1–149; 5 at E–1–285; 5 at E–1–290; 16 at E–1–306; 5 at E–1–387; 5 at E–1–611; 1 at E–2–343; 1 at E–2–382.

DISCUSSION: One specimen preserved in formaldehyde has a body colored pale lemon yellow, intensifying to bright lemon yellow on the legs. The anterior region of the carapace and the antennular and antennal bases are orange-red; the small and especially the large chelae are lemon yellow at the proximal ends, changing to almost blood red at the tips. Some other specimens show a similar color pattern except that the red of the tips of the chelae is restricted to irregular patches surrounded by white. It is not known how well this pigmentation parallels that found in the living specimens.

Crinitus Subgroup

Alpheus alcyone de Man

Alpheus alcyone de Man, Senckenb. Naturf. Gesell. Abhandl. 25: 870, pl. 27, fig. 61, 1902.

Alpheus aculeipes Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 892, pl. 79, fig. 31, 1905.

Alpheus alcyone de Man, Siboga Exped. 39a[1] (2): 351.

LOCALITIES: One specimen at E–1–285; 1 at E–1–611; 1 at E–1–617; 1 at E–1–648; 5 at E–2–382.

Alpheus arnoa sp. nov.

Fig. 5

TYPE SPECIMEN: A non-ovigerous female, 12.2 mm. long, collected on Arno Atoll, Marshall Islands, by R. W. Hiatt at station E–2–343. Only specimen known.

DESCRIPTION: Frontal region of carapace extending considerably beyond eyes. Rostrum short, triangular, reaching about 0.5 the length of visible portion of first antennular article; dorsally bearing a strong and abrupt carina that extends to slightly posterior of gastric region. Orbital hoods rounded, somewhat inflated, anteromedially extending into flattened area, at highest about equal in height to dorsal carina, laterally demarked by an abrupt groove from carapace which covers base of antennal peduncle. Orbitocarinal groove shallow and rounded; orbitorostral area flattened.

Second antennular article slightly less than twice as long as broad, 1.5 times as long as visible portion of first article, 1.7 times as long as third article; diameter only 0.6 that of the first article. Stylocerite acute, with tip reaching almost to end of first article. Basicerite unarmed. Scaphocerite with lateral margin strongly concave, spine heavy, somewhat blunt, reaching beyond end of antennular peduncle; squamous portion narrow and shorter, reaching to middle of third antennular article. Carpocerite reaching to end of scaphocerite.

Large chela subcylindrical, slightly tapering, entire, 2.8 times as long as broad, with the fingers occupying the distal 0.3. Dactylus arched and rounded, calcified and white distally. Tip of fixed finger similarly calcified. Merus 0.37 as long as chela, with outer face 1.8 times as long as broad; all margins unarmed, but inferior internal margin projecting into a low but strong extension. Chela with only sparse scattered setae. Small chela 3.5 times as long as broad, with simple conical fingers occupying the distal 0.38. Carpus somewhat elongate. Merus slightly longer (about 10%) than that of large cheliped, 2.5 times as long as broad, also unarmed. Chela bearing a moderate growth of setae on superior distal face.

Carpus of second legs with the ratio: 10: 21:8:7:11.

Ischium of third legs bearing strong tooth. Merus 4 times as long as broad, armed with a strong acute tooth distally. Carpus unarmed except for poorly developed distal inferior tooth, 0.3 as long as merus. Propodus 3.5 times as long as broad, 0.66 as long as merus, armed on inferior margin with five strong spines and five weaker spines. Propodus and dactylus with usual scattered sparse setae. Dactylus curved, simple, and well developed. Fourth legs of similar armature and proportions.

Telson 2.4 times as long as posterior margin is broad, anteriorly 1.4 times as broad as posteriorly, sides with slight taper; anterior pair of dorsal spines 0.39, posterior pair 0.60 of length posterior from articulation; distal lateral spines moderately strong; strongly arcuate distal margins armed with numerous short heavy spines. Outer uropod with strong lateral spine and with distal margin armed with numerous shorter spines in addition to usual setae. Inner uropod bearing eight strong spines on distolateral margin and numerous short heavy spines similar to those of the telson along distal margin.

DISCUSSION: This species belongs to the Crinitus subgroup, and within the subgroup it appears to be most closely related to those other species with an extended dorsal carina, *A. bucephaloides* Nobili, *A. longecarinatus* Hilgendorf, and *A. parvus* de Man. From the first two species it can most easily be distinguished by the lack of spines on the carpus of the third legs. *A. parvus* lacks the armature of the carpus, like this species, but the configuration of the anterior margin of the cara-

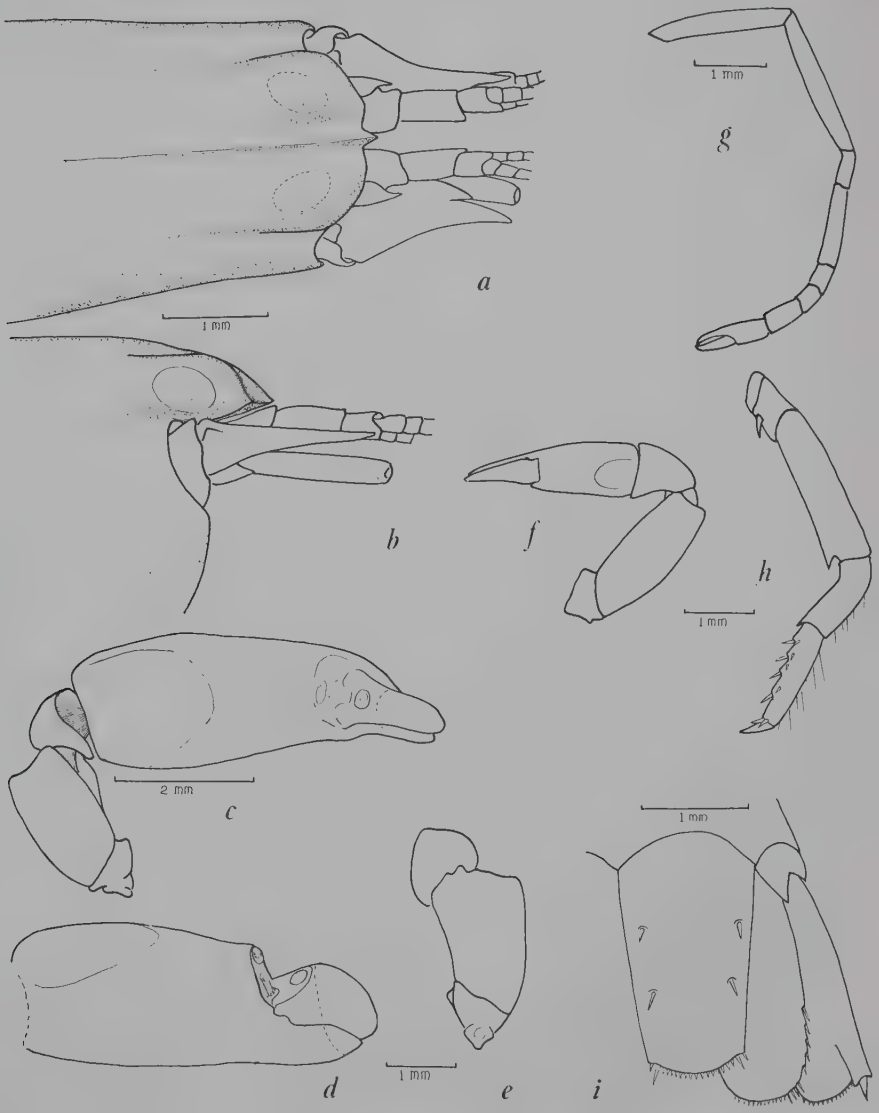

FIG. 5. *Alpheus arnoa* sp. nov. *a*, *b*, Anterior body region; *c*, large cheliped, lateral aspect; *d*, large chela, inferior aspect; *e*, large cheliped, merus, medial aspect; *f*, small cheliped; *g*, second leg; *h*, third leg; *i*, telson and uropods.

pace is different, (compare Fig. 5*a* to de Man, 1911, pl. 15, fig. 74), the flattened portion of the scaphocerite is longer and more narrow, the second carpal article is only 1.3 instead of 2.1 times as long as the first, the telson is more tapering and the spines and spinules of the uropods and telson were unreported by de Man.

The specific name refers to the type locality.

Alpheus bucephalus Coutière

Alpheus bucephalus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 890, pl. 78, fig. 29, 1905.

Alpheus consobrinus de Man, Leyden Rijks Mus. van Naturlijke Hist. Zool. Meded., Notes 30:101, 1908.

Alpheus consobrinus de Man, Siboga Exped. 39a[1]: 360, pl. 16, fig. 75, 1911.

LOCALITIES: One specimen at E–1–122; 11 at E–1–306; 4 at E–2–360.

DISCUSSION: *A. consobrinus* was recognized by de Man as being closely related to *A. bucephalus* and *A. clypeatus* Coutière, but was separated by him on the basis of the following characteristics:

1. The scaphocerite is slightly longer than the carpocerite in *A. consobrinus* and slightly shorter in *A. bucephalus*.

2. The basicerite is armed with a minute tooth in *A. consobrinus* and unarmed in *A. bucephalus*.

3. The merus of the large chela bears an acute tooth on the inferior internal margin in *A. consobrinus* while in *A. bucephalus* the corresponding projection is rounded.

4. The small chela is usually dimorphic in *A. consobrinus*, the males bearing an expanded dactylus with a fringe of setae, while in *A. bucephalus* the dactylus of the small chela of the male is narrow, conical and without a fringe of setae, a condition similar to that of the females.

5. The second article of the second leg is three times the length of the first in the males of *A. consobrinus* while in both sexes of *A. bucephalus* (according to de Man's key) it is "more than twice as long as the first." (However, Coutière's figure 29c shows it to be about 2.75 times as long as the first.)

6. The telson is slightly more narrow in *A. consobrinus*, the length-breadth ratio being 2.6, while in *A. bucephalus* where the ratio is 2.2.

This impressive list of differences would lead one to believe that the species are separate and distinct. However as previously reported from Saipan, the broadening of the dactylus of the males is not a constant characteristic. In this series of specimens a group collected at E–1–306 shows that each one of these characteristics is individually variable. In Table 1 a tabulation of these characteristics of 10 intact specimens is given. The relative lengths of the scaphocerite and carpocerite are quite variable; the spine of the basicerite is present in only two specimens; the meral spine of the large chela varies from strong and acute to low and rounded; the dimorphic character of the small chela of the males does not seem to be correlated with size or other characteristics; the ratio of the first two secondary articles of the second leg varies from 1.7, a figure below that of *A. bucephalus*, to 3.5, a figure above that of *A. consobrinus;* and, finally, the telsal length-breadth ratio ranges from 2.1 to 2.9, the last in the smallest specimen. Moreover, the variations are not correlated with each other, so a specimen like *A. consobrinus* in the sexually dimorphic chela does not have the tooth on the basicerite, etc.

These variations parallel or exceed the variations previously reported upon for the closely related *A. clypeatus* Coutière and *A. brevipes* Stimpson (Banner, 1953: 103–110). I believe that when sufficient specimens are examined from all parts of the range of these four nominal species, it is very likely that the species will all be found to be part of a single, very variable species. However, the present series of specimens do not offer enough direct evidence to warrant this lumping except to combine *A. consobrinus* with *A. bucephalus*.

TABLE 1
VARIATION IN ONE SAMPLE OF *Alpheus bucephalus* COUTIÈRE

Sex	Length, mm.	Length of scaphocerite compared to carpocerite	Tooth on basicerite	Tooth on merus of large cheliped	Length of second carpal article ÷ length of first	Telson, length ÷ breadth at base	SMALL CHELA OF MALES								
							Length Palm, mm.	Length Dactyl, mm.	Length Palm ÷ length, Dactylus	Breadth Dactylus at base, mm.	Length Dactylus ÷ breadth	Breadth Dactylus 0.3 distance from base, mm.	Ratio, breadths of Dactylus	Setae	Sexual Dimorphism
♀ *	13.4	equal	abs	strong, acute	1.7	2.2									
♀ *	11.2	scaphocerite longer	pres	strong, acute	2.3	bro-ken									
♀ *	10.3	equal	abs	low, obtuse	2.7	2.3									
♀	6.5	equal	abs	lacking	1.8	2.8	A	B	A/B	C	B/C	D	C/D	..	..
♂	9.3	scaphocerite longer	abs	low, rounded	1.9	2.1		(lacking)					(lacking)		
♂	8.7	carpocerite longer	abs	strong, obtuse	2.5	2.4	1.07	1.04	1.0	0.40	2.7	0.40	1.0	fringe	yes
♂	8.5	carpocerite longer	abs	strong, acute	3.5	2.6	1.15	0.95	1.3	0.29	3.3	0.22	1.4	scattered	no
♂	8.1	scaphocerite longer	abs	strong, acute	2.8	2.5	1.00	1.00	1.0	0.37	2.9	0.37	1.0	fringe	yes
♂	8.1	carpocerite longer	pres	strong, acute	2.9	2.1	1.18	1.33	0.9	0.51	2.6	0.55	0.9	fringe	yes
♂	7.6	carpocerite longer	abs	low, rounded	2.2	2.9	1.00	0.62	1.7	0.29	2.1	0.15	1.9	scattered	no

* Ovigerous females

Alpheus clypeatus Coutière

Alpheus clypeatus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2 (4): 897, pls. 81–82, fig. 36, 1905.

LOCALITIES: Three specimens at E–1–306 (fragmentary and uncertain); 4 at E–1–617; 5 at E–1–648; 4 at E–2–343.

Alpheus pachychirus Stimpson, 1860

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–290.

Alpheus frontalis H. Milne-Edwards, 1837

For synonymy, see Banner, 1956.

LOCALITY: Two specimens at E–1–611.

Diadema Subgroup

Alpheus bidens (Olivier)

Palaemon bidens Olivier, Encyclopédie Méthodique, Histoire Naturelle 8: 663, 1811.
Alpheus bidens H. Milne-Edwards, Histoire Naturelle des Crustacés 2: 353, pl. 24, figs. 11, 12, 1837.
Alpheus tridentatus Zehntner, Rev. Suisse de Zool. 2: 204, pl. 8, fig. 24, 1894.

LOCALITIES: Two specimens at E–2–360; 1 at E–2–382.

DISCUSSION: These specimens show considerable variation from each other despite the fact that there are only three specimens involved. On one specimen the dorsal denticles of the anterior carapace reach almost to the base of the eyes, while the other two are considerably shorter (but not placed as far posteriorly as indicated by de Man, 1911: pl. 17, fig. 80). The rostrum on one does not reach quite to the end of the first antennular article, on the second reaches slightly beyond it, and on the third reaches almost to the middle of the second article. The first antennular article bears one movable spine and two long setae in two of the specimens, but in the third carries one spine on one side and two spines (as shown by de Man) on the opposite article. On the merus of the large chela the armature varies, with one specimen bearing feeble spines on the inferior internal margin, only several exceedingly weak spines on superior margin, while the inferior external margin carried only about 10 poorly developed serrations; on the second specimens the spines of the inferior internal are quite strong, the superior margin carries 7 short but strong spines, and the serrations on inferior external margin are marked; the third specimen is intermediate between these two.

However in other characteristics, these specimens compare sufficiently well to the descriptions of the species that these variations cannot permit one to consider them as other than this species.

Alpheus diadema Dana, 1852

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–149; 1 at E–1–290; 2 at E–2–343; 2 at E–2–360.

Alpheus percyi Coutière

Alpheus percyi Coutière, Soc. Philomath. Paris, Bul. 9(5): 21, 1908.
Alpheus percyi Coutière, Linn. Soc. London, Trans., Zool. II, 17(4): 426, pl. 64, fig. 22, 1921. [Same description, figures added.]

LOCALITY: Two specimens at E–2–382.

DISCUSSION: This specimen agrees very well with the specimens from the Hawaiian archipelago except for the rostrum. In the Hawaiian species the rostrum bears a low, obtuse but definite crest, but in these two specimens the rostrum is dorsally flat and smooth. While Coutière does not discuss this characteristic in his original description, his figures in his 1921 publication (figs. 22, 22[1]) seem to indicate a condition similar to these Marshall specimens. It may be that the Hawaiian specimens will be found to represent a geograph-

ically isolated subspecies, but not enough specimens are known to draw any conclusions as yet.

Alpheus gracilipes Stimpson, 1860

For synonymy, see Banner, 1956.

LOCALITIES: Two specimens at E–1–306; 2 at E–1–387; 3 at E–1–617.

DISCUSSION: Of these 7 specimens, 2 males and 2 females had their small chelae intact; all 4 had the characteristic fringe of hair over the dactylus, but none had their fingers noticeably broadened. These specimens, therefore, are like the form found in Hawaii and not like the form from the Marianas.

Alpheus paracrinitus var. bengalensis Coutière, 1905

For synonymy, see Banner, 1956.

LOCALITY: One specimen at E–1–106.

Edwardsi Group

Alpheus crassimanus Heller

Alpheus crassimanus Heller, Reise der . . . Novara . . . Zool. Theil 2(8): 107, pl. 10, fig. 2, 1865.

LOCALITIES: One specimen at E–1–387; 2 (fragmentary) at E–1–670; 3 at E–2–311.

DISCUSSION: The fragmentary specimens were assigned to this species because those parts remaining were almost identical to specimens of similar size from Hawaii.

One specimen was somewhat unlike the rest with the sculpturing on the large chela deeper and more abrupt, and the second and third legs thinner and more elongate (the merus of the third legs is 6 times as long as broad instead of the reported 4.5 to 5.0 times). However similar variation in the large chela has been reported for Hawaiian specimens (Banner, 1953: 134), and for this comparison, the meri of a group of specimens collected from a single area in Kaneohe Bay, Oahu, Hawaii, were measured, and it was found that the length-breadth ratio varied from 4.5 to 6.0.

Alpheus strenuus Dana

Alpheus strenuus Dana, U. S. Explor. Exped. 13(1): 543, pl. 34, fig. 4, 1852.

LOCALITIES: One specimen at E–2–169; 6 specimens, Arno, records lost.

DISCUSSION: Some of these specimens, the largest I have yet seen, reach a total body length of 57 mm.; Coutière (1905: 913) has reported specimens reaching 95 mm., but his figures included the chelae.

The distinction between this species and *A. audouini* described by Coutière in 1905 appears to be somewhat questionable. Coutière makes the distinction upon the form of the anterior carapace and rostrum, and the form of the large chela, but the distinctions are so fine as to be scarcely apparent in his figures. Considering the variations that have been reported for other species of the genus, these fine distinctions appear to be of dubious validity. Probably the best differentiations may be found in the antennular base, where the median article is 1.5 times the length of the distal article in *A. audouini* and 2 times the length in *A. strenuus;* in the second legs, where the first article is 1.65 times the length of the second in *A. audouini* and 1.0 to 1.2 times the length in *A. strenuus;* and in the merus of the third legs where the length is 4.3 times the breadth in *A. audouini* and 3.7 times the breadth in *A. strenuus*. Even these differences could easily be within the normal range of variation for an inherently variable species.

Alpheus pacificus Dana, 1852

For synonymy, see Banner, 1956.

LOCALITY: Three specimens at E–1–106.

Alpheus dolerus Banner

Alpheus dolerus Banner, Pacific Sci. 10 (3): 362, fig. 2.

LOCALITIES: One specimen each at E–1–617 and E–2–343.

DISCUSSION: While these specimens compare well to the types and paratypes from Saipan, positive identification is impossible because both are females, and males are necessary for identification in this group.

Alpheus parvirostris Dana, 1852

For synonymy, see Banner, 1956.

LOCALITIES: Three specimens at E–1–106; 11 at E–1–122; 9 at E–1–149; 1 at E–1–285; 1 at E–1–290; 6 at E–1–306; 1 at E–1–387; 1 at E–1–611.

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Records of Bioluminescence in the Ocean[1]

BRIAN P. BODEN and ELIZABETH M. KAMPA[2]

DURING THE MONTH of June, 1955, while measurements were being made of the depth of penetration of moonlight into the sea off the Kona Coast (S. W. coast) of the island of Oahu in the Hawaiian group, some information was obtained on bioluminescence in deep water in this region and on the effect of moonlight on the vertical distribution of luminescent organisms. Observations of bioluminescence were also made off San Diego, California, during the month of January, 1956.

An underwater photometer (Kampa, 1955; Snodgrass *et al.*, 1957 in press) designed for work in the deep sonic-scattering layers was used for these measurements. This was equipped with a depth-indicator (Boden *et al.*, 1955) so that a precise knowledge of the depth of the instrument was available at all times. The instrument utilizes a 931-A photomultiplier tube oriented with the sensitive surface facing up. In front of this is a collimating tube at the base of which is a filter-holder for interference filters. The collimator ensures that the 5° useful angle of the filters is not exceeded. At the distal end of this tube is a diffusing plastic disc, which is a true Lambert-type collector—that is, under a uniform sky the intensity (I_θ) collected from the direction Θ would be

$$I_\theta = I_0 \cos \Theta.$$

Thus the instrument measures irradiance. The collimating tube and filter-holder are free-flooding. The dark-current level of the instrument changes less than 0.2 millivolts on the 0–10 millivolt recorder range through the temperature range 10–30°C. It fluctuates about 0.03 millivolts at any particular temperature. The instrument registers down to 1×10^{-6} μ watts/cm^2.

Observations of bioluminescence in surface waters were made off San Diego (Lat. 32° 38′ N., Long. 117° 35′ W.) on the morning of January 18, 1956.

The photometer was lowered with its sensitive surface pointed downward. The sky was cloudless and moonless, and the first cast was made immediately before the beginning of official twilight. Luminescence was clearly visible at the surface at this time, and porpoises were seen to leave bright trails of light in their wakes.

Flashes, or bursts of light, were observed by the instrument, and recorded on a Leeds and Northrup Speedomax recorder, from the surface to a depth of 60 meters. From a depth of about 25 meters downward the flashes were superimposed on the dark-current level of

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the instrument, and at times apparently single flashes reached a level of 2×10^{-3} μ watts/cm^2.

A later cast, with the photometer still pointed downward, revealed that at sunrise (0652 hrs.) the flashes were first recorded at a depth of about 110 meters.[3] All facts known to us indicate that these flashes are generated *in situ* and we interpret them as due to luminescent organisms, possibly both nekton and plankton.

Records of bioluminescence at depth were first made in Hawaii at midnight on the night of June 9, 1955. The moon, three days past the full, had just appeared over the mountains. Its angle of elevation at 2400 hours was 19°. The instrument was lowered without color filters, and total irradiance, as seen by the instrument, was recorded. The sky was partly cloudy, but the moon remained clear throughout the observations.

Figure 1 is a tracing of the actual recording made on the Leeds and Northrup Speedomax recorder. Total irradiance (H) at any depth was obtained from

$$n = k H = \int_0^\infty E S \, d\lambda,$$

where n = recorder reading, E = energy of the source through the wave-length interval $d\lambda$, S = relative spectral sensitivity of the photomultiplier tube through the wave-length interval, $d\lambda$ (300–700 mμ). The value of k was obtained by calibration of the entire instrument against a Bureau of Standards source. The inset shows the relative spectral sensitivity of the 931-A tube used.

The dark-current level of the photometer was reached at 200 meters. From about 50 meters downward numerous brilliant flashes of light were recorded.

At some depths, for example 120–130 meters and 150–170 meters, the background light level appears to have remained constant or to have increased rather than to have decreased with depth.

Many types of luminescent marine animals, e.g., euphausiids, generate a steady glow of light for limited periods in contrast with the discrete flashes produced by others (Harvey, 1940). Possibly the sustained light level (Fig. 1) on which the flashes are superimposed at depths of 120–130 meters and 150–170 meters was due to a background glow produced by concentrations of such types, or by numerous flashes at varying distances.

An alternative explanation of the flashes can be found by visualizing a distribution of steadily-glowing organisms similar to that of stars in the sky, and a flashlike increase in the level of light due simply to the instrument's approach to and retreat from a glow during its descent. The rate of descent of the instrument was about 32 meters/minute. For this to be the true explanation, the glows would have had to be about 1 meter of depth apart, for the frequency of the flashes was about 36/minute.

Many luminescent organisms flash brightly when irritated mechanically or chemically. It is impossible at present to determine whether the observed flashes were due to spontaneous luminescence or whether the luminescence was intensified by agitation of the animals by the instrument.

Four more casts were made, using narrow-band interference filters, during the forty-five minutes after midnight. The angle of eleva-

[3] The possibility that these are artifacts due to instrument failure is to be considered. It is improbable that distortion due to pressure affected the circuitry, for the phenomenon was not observed when the instrument had been lowered to greater depths during daylight. It is improbable, too, that the effect could have been caused by water leakage, for moisture in the system has been shown to raise the dark current to such a high level that the recorder is immediately sent off scale. Furthermore the fact that color filters placed in the light-path reduced the amplitude of recorded flashes discounts the possibility that loose electrical connections were responsible. Another photometer, similar to the one employed here, has since shown that the flashes are not recorded when the sensitive element is covered but are when it is exposed immediately afterward at the same depth. Thus we believe that the instrument was sensing real light flashes.

Flashes of this nature could not have been caused by tilt of the instrument since it was pointed downward.

tion of the moon varied between 21° and 31° during this period. The interference filters employed were G. A. B. filters, manufactured in Liechtenstein, with half-peak band widths of about 10 mμ. Block filters are incorporated to reduce stray light and eliminate secondary transmission peaks. Peak transmissions, measured by a Beckman Model DU spectrophotom-

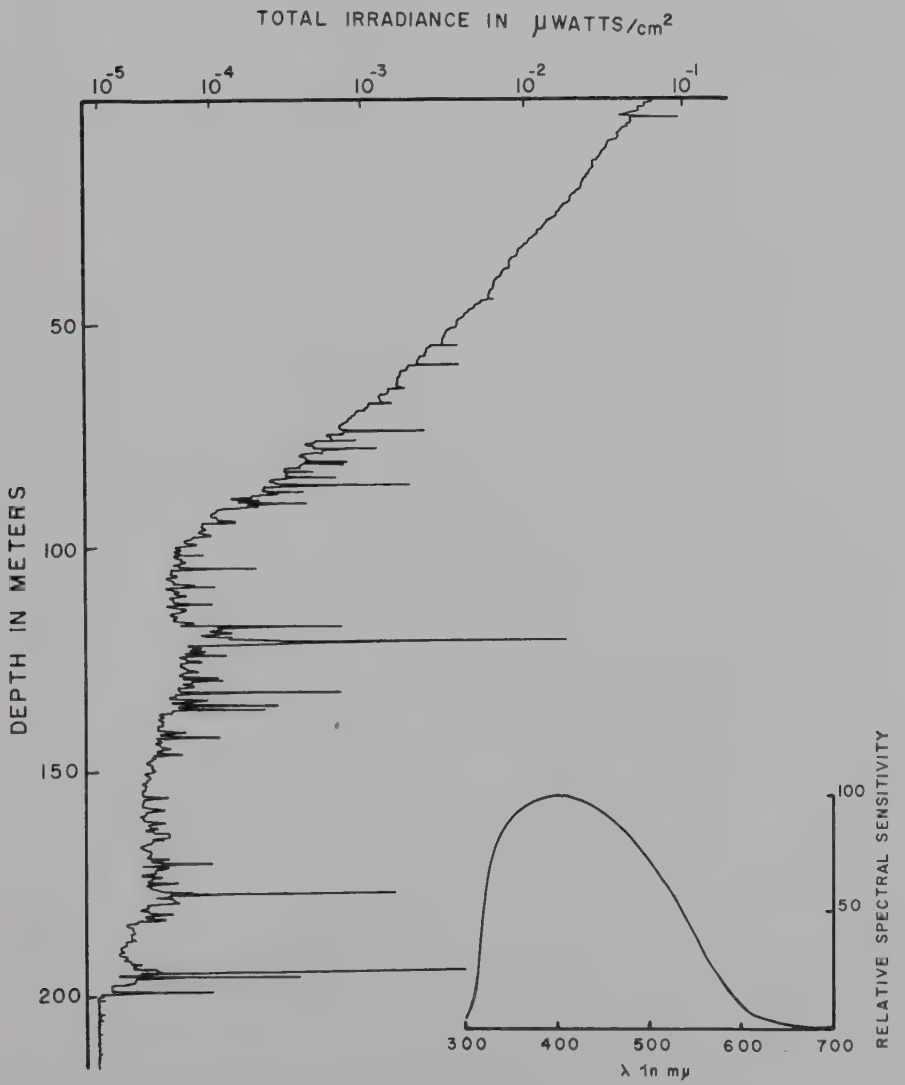

Fig. 1. Tracing of total irradiance recorded on Leeds and Northrup Speedomax recorder by bathyphotometer without color filters. Spectral sensitivity of the 931-A photomultiplier tube is shown in inset. This is from manufacturer's specifications and is an average curve. The record was made at 2400 hours, June 9, southwest of Oahu.

eter, are at 418, 491, 552, and 630 mμ (see inserts in Fig. 2).

Irradiance (H) was obtained from

$$n = k H = \int E T_f S \, d\lambda,$$

where n = recorder reading, E = energy of the source through the wave-length interval $d\lambda$, T_f = measured transmission of the individual interference filter through the wave-length interval $d\lambda$, and S = the relative sensitivity of the photomultiplier tube through the wave-length interval $d\lambda$. The value of k was obtained as indicated above.

Tracings of the recordings are shown in Figure 2. Orange light (λ max, 630 mμ) is seen to cut out at 11 meters, and no flashes are apparent. With the 418 mμ filter, the dark-current level of the instrument was reached at a depth of 280 meters.

The 418 mμ cast reveals an actual increase in irradiance with depth between 100 and 220 meters. Sudden flashes again occurred between 100 and 280 meters, but these, as recorded, were of lower amplitude than those in the unfiltered cast, presumably because of the narrowness and reduced intensity of the transmitted band.

These observations indicate that the light generated at depth is blue-violet (see Harvey, 1940, for spectral distribution of bioluminescence). It can be seen too (Fig. 2) that the flashes produced in the surface layers are greener.

The greater depth attained with a 418 mμ filter in the instrument (cf. Figs. 1 and 2) and the deeper flashes may be explained on the assumption that some of the light-generating constituents of the population had by then sought greater depths as the moon cleared the mountains and approached its zenith. The possibility that these constituents comprise a photoregulated community similar to the Californian deep-scattering layer may be inferred from this assumed downward migration with increasing illumination.

This inference is substantiated by observations made off San Diego (Lat. 32° 38′ N., Long. 117° 35′ W.) on January 17, 1956. At this time EDO fathograms and light measurements were made simultaneously during the periods of the twilight migration of the sonic-scattering layer. Figure 3A (1640–1650 hours) shows that flashes were first recorded as the photometer reached the depth of the scattering layer. Thirty minutes later (1720–1728 hours) the top of the scattering layer had reached a depth of 120 meters. Figure 3B shows that the first flashes recorded by the photometer were now at this same depth. On the day of these observations sunset was at 1706 hours.

We have recorded flashes, during our scattering-layer studies, in the Pacific, Atlantic and Mediterranean. They appear to increase both in frequency and amplitude during the twilight migration of the layer and at night. On this account it is extremely difficult to obtain an accurate picture of the spectral distribution of moonlight in the sea, or even of sunlight at scattering-layer depths.

Since the completion of this paper we have heard from Professor George L. Clarke of Harvard University (Clarke and Backus, in preparation) that he too has recorded flashes of luminescence off the Florida coast.

This phase of work on the sonic-scattering layers received additional support from the National Science Foundation and the Pauley Fund of the University of California. The inquiry was pursued from the Marine Laboratory of the University of Hawaii. The Californian data were obtained from the "USS EPCE(R) 855." Acknowledgment is made of the generous loan of the Research Vessel "Makua" by Mr. Vernon Brock, Director of the Territorial Fish and Game Commission, Hawaii. The U. S. Air Force and Marine Corps were unstinting in their loan of equipment and facilities. Data were analyzed and most of this paper was written at The Laboratory, Plymouth, England. The hospitality of the director, Mr. F. S. Russell, F. R. S., is most gratefully acknowledged. Professors

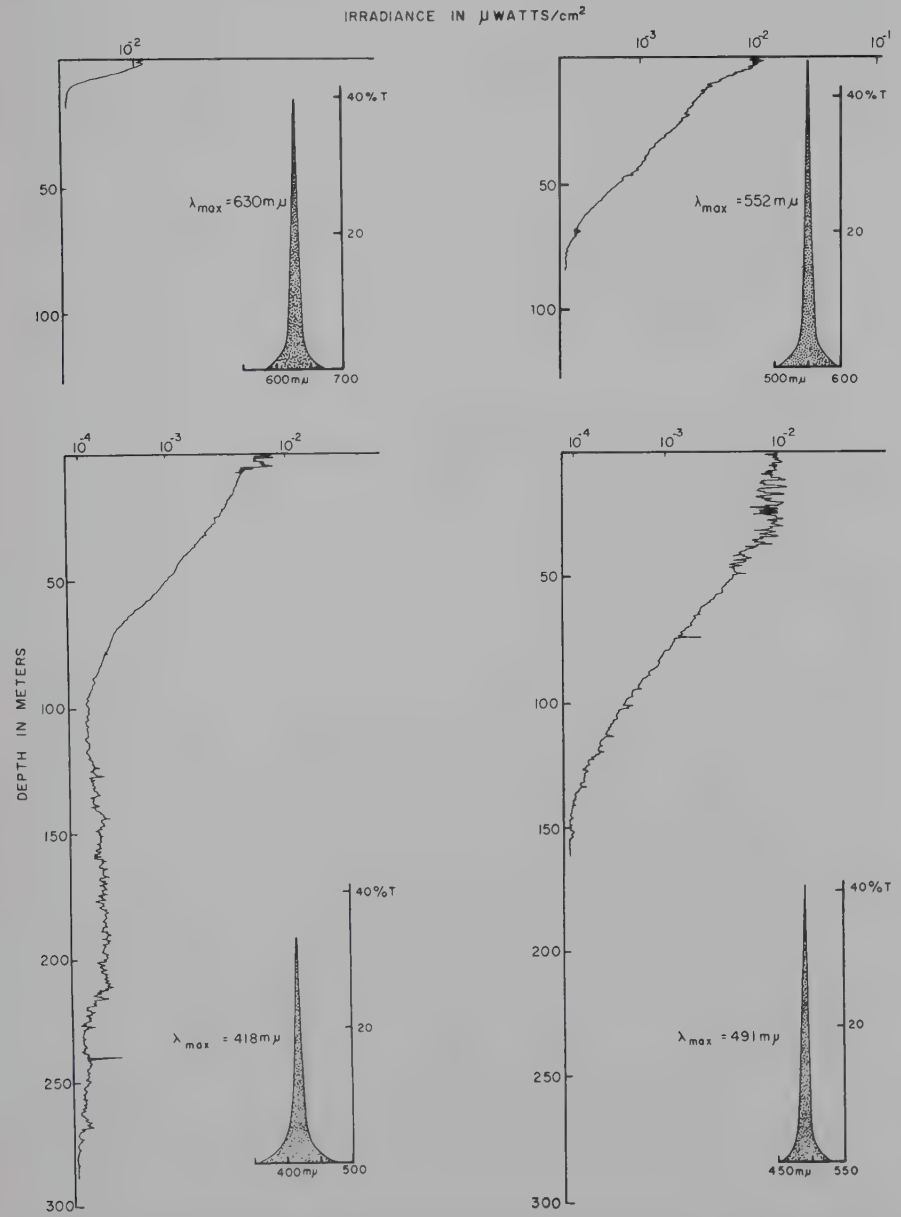

Fig. 2. Tracings of irradiance record at four different wave lengths as determined by bathyphotometer using interference filters. Insets show measured transmission curves of filters used. The records were made at the following times: 630 mμ—0020 hrs.; 552 mμ—0030 hrs.; 491 mμ—0044 hrs.; 418 mμ—0058 hrs.; all on June 10, southwest of Oahu.

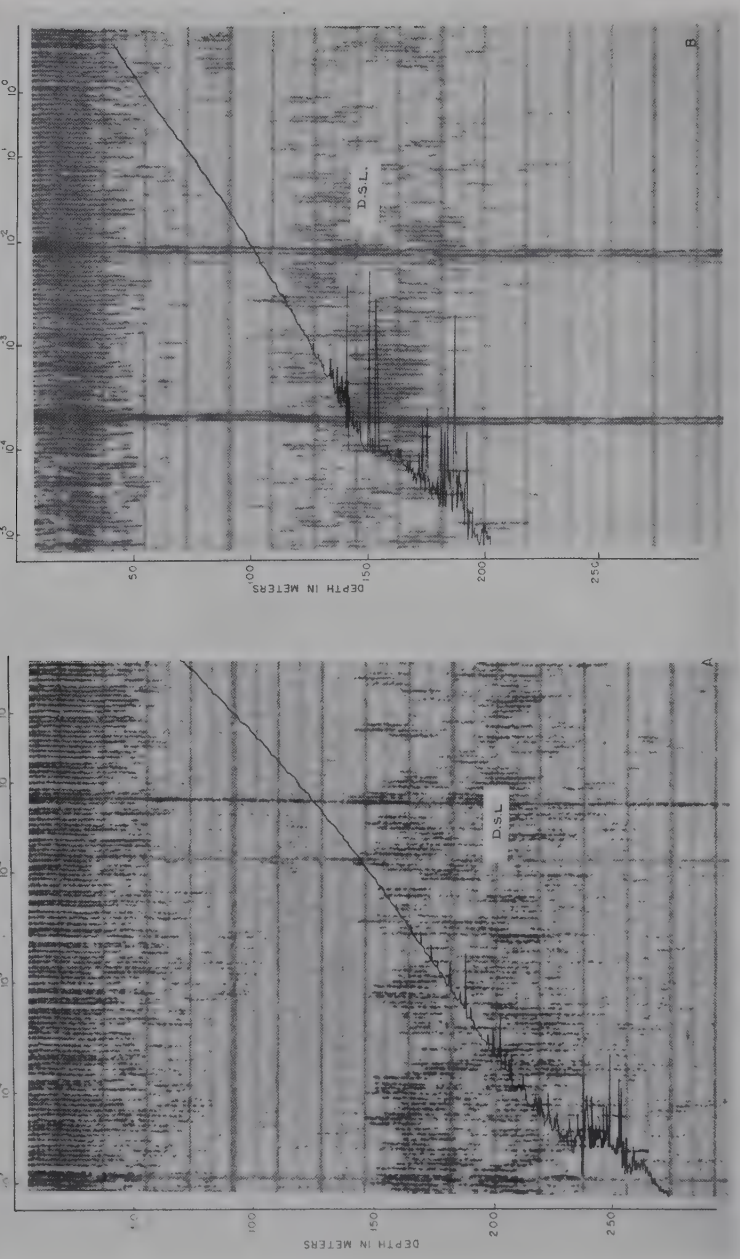

FIG. 3. Tracing of total irradiance recorded 17 January 1956, in the San Diego Trough, Latitude: 32° 38′ North; Longitude: 117° 35′ West. The superimposed fathograms were recorded at the same time. A: 1640–1650 hrs., B: 1720–1728 hrs. The light curve does not reach the surface because the upper limit of the photometer's range is about 2μ watts/cm².

Carl Eckart and Carl L. Hubbs of the Scripps Institution and Mr. John Tyler of the Visibility Laboratory of the Scripps Institution subjected the manuscript to vigorous and stimulating criticism.

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OBSERVATIONS ON THE OSMOREGULATION IN *APLYSIA JULIANA* PEASE (APLYSIIDAE, MOLLUSCA)

By

P. B. van Weel

With 3 Figures in the text

(Eingegangen am 15. Januar 1957)

* Contribution No. 91, Hawaii Marine Laboratory.

It is a well established fact that the integument of aquatic animals is not only permeable to water (Frédérique 1901, Botazzi 1908), but often also to certain ions and molecules (Krogh 1939). The permeation of salts is as a rule, however, markedly slower than that of water. It has also become apparent that, with respect to the compensation of the osmotic pressure after transferring marine animals to either diluted, or concentrated sea water, there is need to distinguish between the so-called *osmoadjustors* and the *osmoregulators*. The former are organisms which reach the new state of osmotic equilibrium passively, without the expenditure of energy, whereas the latter actively try, with more or less success, to maintain the original osmotic pressure of their body fluids despite an existing osmotic gradient. This, of course, cannot be achieved without expending energy.

Bethe (1929, 1930, 1934), in his classic experiments with *Aplysia*, arrived at the conclusion that this organism belonged to the osmoadjustors, but that its integument behaved like a "leaking" membrane of an osmometer: water permeated freely and rapidly. Salts also permeate, but apparently at a much slower rate. He claimed that even sugar molecules seemed to be able to pass the "membrane". When *Aplysia* was transferred to diluted sea water, first a rapid increase in weight occurred, due to the osmotically directed influx of water. This increase in weight was then followed by a decrease, because more and more salts from the body fluid diffused slowly out of the body, until in about 6 –8 hours an equilibrium was reached. When transferred to an isotonic sugar solution *Aplysia* lost weight continuously, not-withstanding the isotonicity between blood and outer medium: the animal lost salt by diffusion out of the body. The result was that the blood became hypotonic to the surrounding medium and water consequently left the body. When the animal was brought back into normal sea water after a stay in isotonic

sugar solution, its weight increased and became even slightly higher than the initial weight. This indicated that sugar had diffused into the blood, making it hypertonic to sea water.

Although Bethe's data appear rather conclusive and his explanation sound, subsequent reflexion on the concequences of his conception soon casts some grave doubt on its validity. If *Aplysia* was merely a "leaky" osmoadjustor, then what would happen if it was subjected to changes in the salinity of sea water over a longer period of time? What would result, if the animal would be exposed alternately to diluted and 100% sea water? Such conditions do occur in shallow water and particularly in tide pools during the rainy season, when at low tide the sea water becomes diluted and this diluted water is replaced at high tide quite suddenly by 100% sea water. Bethe showed that, when equilibrium was reached in diluted sea water and the animal was transferred to 100% sea water, its weight declined rapidly (loss of water) and reached a *steady level* at a much lower value in a short time. This equilibrium was reached far more rapidly than that in diluted sea water. When no compensating mechanism was present (as would be the case in a "pure" osmoadjustor), then the animal, in its natural habitat, should become smaller and smaller. This is apparently not the case, at least not with the Hawaiian Aplysiidae.

Another reflexion which casts some doubt on the validity of Bethe's conception, is presented by his own data: Often the weight of the animal, after reaching the equilibrium in diluted sea water, was and remained appreciably higher (10—12%) than its initial weight. At other times it appeared lower by about 15%. One would expect to find the same weight as the initial one after it reached the osmotic equilibrium.

To these considerations should be added the fact that these animals have a comparatively well developed excretory system (kidney). The presence of such a kidney suggests that this organ *might* play some role in the elimination of excess water and that it does not serve solely to eliminate metabolic wastes. It seems therefore not too bold to assume that *Aplysia* may attempt to regulate the osmotic pressure of its body fluids, but apparently, according to Bethe's results, without much success. If this assumption be correct, than such an active regulation should become apparent in its oxygen consumption: increasing activity results in increasing metabolism, hence an increase in oxygen consumption. In order to test this idea, Bethe's experiments were repeated, but at the same time oxygen consumption was determined.

Material and technique

The experimental animal, *Aplysia juliana* Pease, is quite common in the shallow waters of Oahu and is found particularly where the water is comparatively quiet

and where algal growth (predominantly *Ulva*) is abundant. Animals of 30—45 grs., to be used in the experiments, were kept well fed. Preliminary experiments proved this to be of importance, since the results obtained with starving *Tethys* showed a very wide spread of the experimental data. Before starting an experiment the animals were weighed (after superficial drying with a towel), after which they were placed in a respiration vessel of about 600 cm³. From one of two carboys 100% sea water, flowing at a constant rate of 6 L./hour, entered the respiration vessels (fig. 1, *RV*) at the bottom and left them at the top. A piece of screening wire (fig. 1, *S*) fitted over the "outflow" tube, prevented the animal from inadvertantly plugging the outflow. A large funnel (fig. 1, *F*) about 30 cm above the respiration bessels, served as an overflow and provided a steady head of water pressure. By manipulating the screw clamps SC_3 and SC_4 the rate of the flow was regulated. By opening or closing the clamps SC_1 and SC_2, either 100% or diluted sea water could be admitted at a rate just fast enough to cause the water, flowing into the funnel, to drip slowly over the funnel's rim. Screw clamp SC_5 allowed a sample of water to be taken directly from the carboys to determine its oxygen content and salinity before entering the respiration vessels. Clamp *SC* was open during the experiments but necessarily closed when animals were placed into or removed from the respiration vessels to prevent air from entering the "inflow" tubes. Care was taken that none of the tubes, leading from the funnel, or the respiration vessels, contained air bubbles. The oxygen content of the inflowing and of the outflowing water was determined with Winkler's titration method, after the animal remained for 30 minutes to one hour in the undiluted sea water. The salinity of the sea water was determined in the usual way ($AgNO_3$ titration with K-chromate as an indicator). Then the diluted sea water was allowed to flow through the respiration vessels for a period of a certain length, after which again the oxygen content of in- and outflowing water was determined. The periods of time, during which the animals remained in the diluted water, were: 0.5, 1, 2, 3, 5 and 6 hours in the first series; 0.5, 1, 2, 3 and 5 hours in the second series of experiments. Because the carboys contained a little less than 20 L. each, the animals were placed in a separate container filled with the same diluted and continuously aerated sea water first in all experiments, where their stay in diluted sea water exceeded 1 hour. Half an hour before their stay in diluted sea water ended, they were quickly transferred to the respiration vessels, which were previously filled with diluted sea water. After staying here for the designated period in diluted sea water, the animals were removed, quickly dried, weighed and finally bled. Care had to be taken that the blood

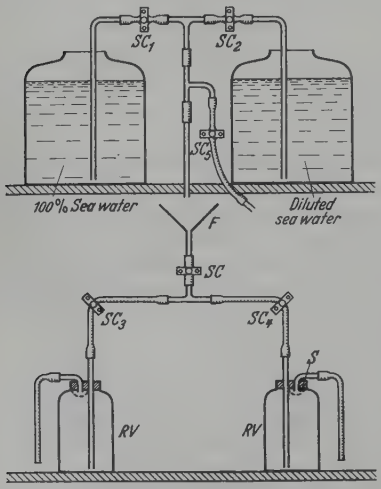

Fig. 1. Apparatus for the determination of the oxygen consumption in a continuous flow of water at a constant rat

was not contaminated with the milky white secretion the animals extrude when handled roughly or when wounded. As a rule the blood appeared to be nearly colorless. Only a few times was it decidedly blueish. The salinity of the blood was also determined.

In the second half of each series of experiments the same routine was followed, but the animals were first forced to stay for 5.5 and 5 hours respectively in diluted sea water, after which they were weighed, then transferred to 100% sea water. Here they were allowed to stay for 0.5, 1, 1,5, 2, 3, 5, 6, 7, 17, and 0.5, 1, 2, 3, 4, 6, 7, 18 hours respectively.

For the first series of experiments 80% sea water, for the second series 95% sea water was used as diluted sea water. The extremes of temperature encountered throughout all experiments were 25.8° C and 27.0° C, but as a rule the temperatures were between 25.8° C and 26.4° C and during one and the same experiment never changed for more than 0.5° C.

Experimental results

Series AI (table 1). Effect of 80% sea water on weight, salinity of the blood and oxygen consumption of *Aplysia* during a stay of varying length in this diluted sea water.

The spread of the data of the O_2 consumption is extensive. Less that of the changes in weight, whereas the data of the salinity of the blood appear quite satisfactory.

Table 1

stay in dil. sea water in hours	I*	II*	III*	IV*	stay in dil. sea water in hours	I*	II*	III*	IV*
0.5	0.18	350	116	81	4	1.34	54	106	81
	0.08	525	118**	83		1.11	24	120	81
1	0.63	131	107	81	5	0.42	86	112	81
	1.31	177	125	81		0.76	36	112	81
	0.72	136	109	80	6	0.46	46	112	81
3	0.26	104	121	79		0.40	50	110	80
	0.35	81	119	78					
	0.77	55	116	82					
	0.63	67	113	81					

* All data represent the means of 2 readings. I: initial O_2 consumption in 100% sea water in cm^3 O_2/L. — II: O_2 consumption in diluted sea water in % of that in 100% sea water. — III: weight after stay in diluted sea water in % of the initial weight. — IV: salinity of blood after stay in diluted sea water in % of that of 100% sea water.

** In one experiment, which had to be discarded because of contamination of the blood with the milky secretion, the weight of the animal was 850%, compared with its initial weight. The oxygen consumption was more than 1200%. Such an exceptional increase in weight and O_2 consumption was only met once.

Series AII (table 2). Effect of 100% sea water on weight, oxygen consumption and salinity of the blood after a stay of 5.5 hours in 80% sea water.

Here again the data show an extensive spread, except those of the blood salinity. In fact, the spread of data obtained is so large, that grave

Table 2

stay in 100 % sea water in hours	initial O_2 consumption in 100 % sea water	I*	II*	III*	IV*	V*
0.5	0.55	13	71	98	92	83
	0.41	43	46	103	81	85
	0.38	51	40	101	85	80
1	0.33	45	52	101	82	93
	0.36	35	43	103	80	91
1.5	0.85	15	19	115	107	98
	1.37	18	18	117	108	96
2	0.75	57	40	87	70	98
	0.48	50	42	90	69	99
3	0.77	47	32	113	92	100
	0.91	45	33	118	84	94
5	0.87	32	37	121	89	98
	1.05	16	16	120	51	99
6	0.80	30	28	122	64	99
	0.95	52	18	136	79	99
7	0.73	51	23	124	81	99
	0.56	46	29	123	100	98
17	0.59	37	†	125	†	†
	0.44	52	†	119	†	†

* The data are the average of 2 determinations. I: O_2 consumption at the end of the stay in diluted sea water, in % of the initial O_2 consumption. — II: O_2 consumption at the end of the stay in 100% sea water, in % of the initial value. — III: weight at the end of the stay in diluted sea water, in % of the initial weight. — IV: weight at the end of the stay in 100% sea water, in % of the initial weight. — V: salinity of the blood at the end of the stay in 100% sea water, in % of salinity of 100% sea water.

doubt arises concerning their validity in so far as that they would represent data obtained from *normal* animals. This must indeed be denied. Already after a stay of 3 hours in 80% sea water they appear to be in a very poor state: They are definitely oedematic and show little movement, if at all. Their foot seems to lose its "grip", so that the animal invariably turns upside-down and lies on its back. After a stay of 5.5—6 hours in 80% sea water they appear practically without any movement. Even the parapodia have ceased their motility. The strongly reduced oxygen consumption also suggests a very poor condition. Transfer to 100% sea water does not revive them. Indeed, they die after a stay in 100% sea water of about 9—12 hours (see last experiment, table 2). These results clearly demonstrate that 80% sea water is too much diluted for *Aplysia* to be able to live in and that *a stay of 5.5 hours inflicts irreparable damage to the animal*. Therefore the experiments were repeated, now using a dilution of 95% sea water.

Series BI (table 3). Effect of 95% sea water on weight, oxygen consumption and salinity of the blood during a stay of varying length in the diluted sea water.

Table 3

stay in dil. sea water in hours	I*	II*	III*	IV*	stay in dil. sea water in hours	I*	II*	III*	IV*
0.5	0.66	103	104	96	3	0.77	108	105	97
	0.30	120	103	97		0.59	98	100	96
1	0.69	154	103	95		0.69	112	105	97
	0.66	133	105	98	5	1.01	119	108	96
2	0.84	123	103	97		0.56	116	105	96
	0.80	117	104	97		1.04	98	98	95

* All data represent the mean of 2 determinations. I: initial O_2 consumption in 100% sea water in cm^3 O_2/L. — II: O_2 consumption at the end of the stay in 95% sea water, in % of the initial O_2 consumption. — III: weight at the end of the stay in 95% sea water, in % of the initial weight. — IV: salinity of the blood at the end of the stay in 95% sea water, in % of the salinity of 100% sea water.

Table 4

stay in 100 % sea water in hours	initial O_2 consumption in 100 % sea water in cm^3 O_2/L	I*	II*	III*	IV*	V*
0.5	1.04	97	96	95	92	98
	0.79	105	102	100	86	98
1	0.75	121	88	106	74	98
	0.67	131	107	110	81	99
2	0.62	103	98	98	80	100
	0.45	108	96	104	75	100
3	0.55	116	140	99	93	100
	0.63	102	136	102	90	100
4	1.03	104	154	105	99	99
	1.34	98	160	109	97	100
6	0.44	120	164	102	96	100
	0.37	102	178	108	99	100
7	0.93	116	110	98	98	100
	0.57	104	100	103	100	100
18	0.65	108	100	99	99	100
	0.59	119	101	102	100	100

* All data are the mean of 2 determinations. I: O_2 consumption at the end of the 5-hours stay in 95% sea water, in % of the initial O_2 consumption. — II: O_2 consumption at the end of the stay in 100% sea water, in % of the initial O_2 consumption. — III: weight at the end of the 5-hours stay in 95% sea water, in % of the initial weight. — IV: weight at the end of the stay in 100% sea water, in % of the initial weight. — V: salinity of the blood at the end of the stay in 100% sea water, in % of the salinity of 100% sea water.

Series BII (table 4). Effect of 100% sea water on weight, oxygen consumption and salinity of the blood after a 5-hours stay in 95% sea water.

Discussion

A few objections to BETHE's assumption of *Aplysia* being an osmoadjustor have been raised already in the introduction of this paper. Some of his data which seem to contradict his conception, are those which indicate some animals to become lighter than the initial weight after osmotic equilibrium in diluted (75%) sea water has been established. This certainly does not point toward a passive adjustment by a "leaky" osmometer. As mentioned before, we would expect the animal to attain at equilibrium the initial weight. The fact that part of his animals are lighter point rather to an active removal of water.

Another objection which may be raised is that BETHE used dilutions of 75% sea water, dilutions which seem to be rather unphysiological to use for animals which normally do not live in brackish water. It is quite possible that under such severe conditions the results obtained do not reflect normal responses of the animal, but may represent definite pathological conditions.

The results, obtained in the first two series of experiments (series AI and AII) reported upon in this paper, do show that at least in *Aplysia juliana* some irreparable damage to the organisms is inflicted when they are subjected to a stay of 5—5.5 hours in 80% sea water (which is even more concentrated than the sea water BETHE used). The very wide spread of the data under these experimental conditions, which were kept as constant as possible, suggests already that something seems to be abnormal. It may be questioned even, whether the data obtained in the various stages, are indeed significantly different from each other. However, by drawing the main course of the curves, based on the results of series AI and AII, it is obvious that the results of changes in weight and salinity of the blood run closely parallel to those of BETHE (fig. 2): in the weight curve we first get a rapid increase until a maximum is reached, which is maintained during the entire stay in the diluted water. BETHE reported an increase, followed by a decrease in weight, but in some of his curves the decrease is very small. In a few cases of the experiments reported here, a decrease following the increase has indeed been found, but since the curve is based on the average of all values, which show such a wide spread, this does not show in fig. 2. When transferred back to 100% sea water the same steep decline of the curve appears as BETHE has reported, until a steady level is reached, where the weight does not change any more. The animals are solid to the touch with a marked increase in tonus. In many cases they even seem to appear in a state of mild contracture. Movement has practically ceased.

The curve of the salinity of the blood follows a course exactly like Bethe reported: a quick drop to about 80% when the animals are brought into diluted sea water, a quick rise when transferred from here to 100% sea water. The results of the determinations of the oxygen consumption show, however, that the effect of the highly diluted sea water on *Aplysia* causes positively abnormal results: as soon as the animal is transferred to 80% sea water there occurs an enormous increase in oxygen consumption (fig. 2), indicating a sharply increased metabolic rate, a positive signal for increased activity. This steep increase is without any doubt partly caused by the increased motility of the animal. As soon as it gets into the diluted sea water it starts to move about restlessly, to quiet down in about 30 minutes. Very probably other increased organ activity adds to the uptake of oxygen, because moving animals in 100% sea water never show such an enormous increase in oxygen consumption. After 30 minutes, when the animal has quieted, there is an equally rapid drop in oxygen consumption, which slows down after about 1 hour, *but the oxygen curve continues to slope down during the entire duration of the experiment.* Even when the animals are transferred back to 100% sea water after a stay of 5.5 hours in diluted sea water! Apparently too much damage has been inflicted and the animals, which are in a very poor condition after the stay in the diluted sea water, do not revive. They die between 9—12 hours after being transferred to 100% sea water. Although the possibility cannot be denied that the Mediterranian *Aplysia* may be less sensitive to such high dilutions than *Aplysia juliana*, it seems not very probable. If this latter proves to be correct, than Bethe has worked with abnormal, even dieing animals and his conclusions have little value with respect to the behavior of the *normal* animal.

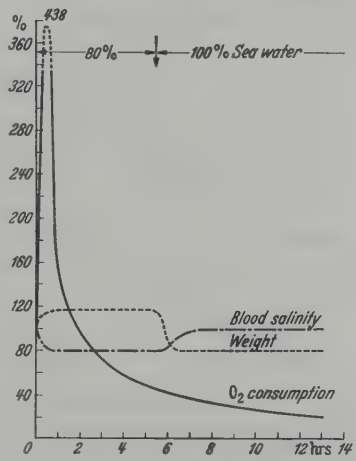

Fig. 2. Changes in weight, consumption of oxygen and salinity of blood during a stay of a certain length of time in 80 % sea water, followed by a stay in 100 % sea water. *Abscissa:* time in hours; *ordinates:* changes in % of the normal, initial value (= 100 %)

A second series of experiments (series BI and BII), now using 95% sea water, which may be considered to be in the physiological range, indeed shows quite different results (fig. 3). On placing the animal in

95% sea water a rapid increase in weight occurs, but this is relatively small, less than 5%. Again in half an hour a steady state, indicating an osmotic equilibrium, is reached and maintained. After transferring the animal to 100% sea water a steep drop in weight is encountered, far greater a loss of weight than would be expected. A new steady state is reached in 1—1.5 hours, after which there occurs an increase in weight, first rapidly, then more slowly, until after about 6—7 hours the initial weight is regained (fig. 3).

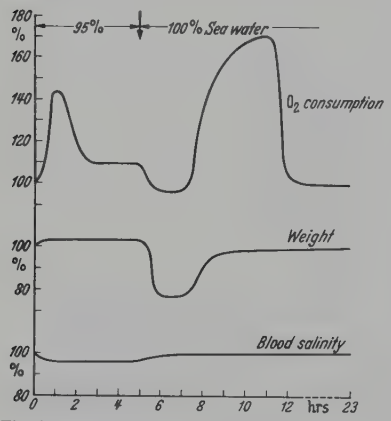

Fig. 3. Changes in weight, consumption of oxygen and salinity of blood caused by 95% sea water and subsequent stay in 100% sea water. *Abscissa* and *ordinates* like in fig. 2

The curve of the salinity of the blood shows first a slight drop, less than would be expected when only osmotic water movements are included in the process, during the first half hour in diluted sea water, whereas the original salinity is quickly reached again when the animal is transferred back to 100% sea water (fig. 3). The oxygen curve shows a distinctly different course from that obtained in the first series: after the first steep (but by far not as high) increase there follows a decrease until a steady level is reached, appreciably higher (about 10%) than the initial value (fig. 3). On transfer to normal sea water the oxygen consumption drops rather sharply to reach a level apparently slightly lower than that of the normal respiration. This level is maintained for about 1 hour, after which there is first a steep, followed by a flatter increase. When the weight increase has practically ended, the oxygen consumption drops quickly to the initial value (fig. 3).

Analysis of the data and the curves shows that (a) the spread is much smaller, although that of the oxygen consumption is sometimes considerable. However, the animals which remain in 95% sea water are much livelier during the entire stay of 5 hours and sometimes move around in the respiration vessels for quite some time. Thus a bigger spread can be anticipated. (b) The salinity of the blood remains in 95% sea water slightly higher than that of the surrounding medium, *showing that a (slight) osmotic gradient is maintained.* This means an increase in expended energy, which is well illustrated by the fact that the oxygen

consumption is at a higher level during the entire period the animal remains in diluted sea water. The initial sharp and high increase of oxygen consumption is certainly, for a great part, caused by the increased motility of the animal when transferred to diluted sea water. The slight increase in weight shows that the rate of excretion of the osmotically inflowing water is not high enough to cope completely with the situation, but it certainly shows that some osmoregulation occurs.

(c) When transferred to 100% sea water after a stay of 5 hours in diluted sea water, both oxygen consumption and weight drop rapidly, whereas the salinity of the blood resumes its original value somewhat slower. The fact that the weight decreases to an appreciably lower value than would be expected, if the change in volume were only caused by osmoadjustment, can be explained in the following way: when transferred to 100% sea water the tonus of the entire animal becomes definitely higher. It feels much more solid to the touch. Apparently a tonic contraction takes place, bringing the body fluid under a higher pressure. It may be possible that this increased pressure causes a passive loss of water (and salts) by "leakage" through the surface and thus causes a greater loss of weight. However, this loss of water needs not, and is probably not only a loss of body fluid (blood). More probable water will be expelled in the first place from the intestine. But the result is an overall loss of weight, higher than expected. The excretory activity can be expected to cease now, because water will leave the body cavities by way of osmotic forces and this is well demonstrated by the drop of oxygen consumption during the same period that the body loses weight. For some time weight and oxygen consumption remain at this low level and during this time the blood, by osmotic loss of water, regains its initial concentration. Its volume has, however, become smaller now. As soon as this salt concentration is reached, a new process appears: the body weight increases, first rather rapidly, than more slowly, until the original weight is regained in about 6—7 hours after transfer to 100% sea water (fig. 3). This increase in weight cannot be explained in terms of osmotic forces, because there is isosmoticity between blood and surrounding water when the weight increase begins. *Therefore sea water must be taken in actively*, very probably by way of the intestinal tract. This active water resorption, which apparently brings the volume of the body fluids up to par, is reflected in the steep increase of the oxygen consumption, which starts at the same moment the weight increase begins and drops quickly to the normal, initial value, when the initial weight is reached.

From the experiments it appears that 80% sea water is detrimental to *Aplysia juliana* (which is also the case with *A. grandis* Pease, as some experiments have shown). Irreparable damage is apparently inflicted by

salts were lost during the stay in the highly diluted sea water. This animal seemed to act therefore like a true osmometer. However, this did not mean that salts cannot be lost at all. When placed in a mixture of $^1/_3$ sea water and $^2/_3$ isotonic sucrose solution, the volume reduced by 33% in 14 hours, which showed that under certain conditions salts can be lost (cited from PROSSER *et al.* 1950). An osmoregulative mechanism seemed, however, to be missing in this animal.

From these data it becomes apparent that "pure" osmoadjustment is certainly not wide-spread in molluscs. A certain mechanism of osmoregulation seems to occur more often, a mechanism which is often comparatively very weak, in other cases apparently better developed. But this does not mean that such a weak mechanism is not adequate under *normal* conditions. As a rule the dilutions used in experiments are much more severe than those met in the natural habitat. It is quite possible that the regulative activity is perfectly adequate in normal conditions. Bivalves, like *Mytilus edulis*, which are normally subjected to temporary enormous delutions, although lacking a good osmoregulation, defend themselves by closing their shells tightly under such extreme conditions. MALOEUF (1938) in particular pointed out that when the shells were not forcibly kept open during the experiment, the data obtained showed quite different values, the blood being definitely hypertonic to the surrounding medium. By keeping its shells closed the mussel escapes the danger of over-diluting its body fluids. Thus the means of "defense" of this organism is quite different to that of osmoregulating animals.

Another point should be brought forward, a point which seems to be overlooked too often: generalization of facts obtained at one species can be very dangerous. Even closely related animals may show marked differences in their behavior and reactions to changes in the surrounding medium. This was clearly demonstrated in the following case: When the investigations, reported upon in this paper, were started, *Aplysia grandis* PEASE, being a larger animal, was used. At that time they were plentiful and easy to collect. These experiments had to be terminated after the first stages were investigated because of their sudden disappearance, and *A. juliana* was used in stead. *A. grandis*, now, when placed in 80% sea water, showed a very low increase in weight and in oxygen consumption, compared with *A. juliana* (weight: 109% in 1 hour, after which it decreased to 102%; oxygen consumption: 103—104% during the first 30 minutes, no increase after 1 hour, a decrease to 48% of the initial value after 3 hours). The loss of salts from the blood was comparable with that of *A. juliana*, often even faster. Since *A. grandis* occurs as a rule more often on the reefs somewhat farther away from the shore, it may be that the difference is caused by the fact that the semipermea-

bility of the integument is less well developed, that "leakage" occurs therefore on a larger scale. Although, according to the oxygen consumption, there seems to be also some osmoregulation, it is definitely weaker even than that of *A. juliana*. Now, while living farther sea-ward, the animal will probably not be subjected to dilutions as found nearer to the shore, so it really does not need a better regulative activity. However, more experiments should be performed on *A. grandis* before this suggestion can be accepted as an explanation of the difference in behavior. The few data on hand do serve, however, to show that marked differences do occur between two closely related species with respect to their response to differences in salinity of the surrounding water.

I am very much indebted to Dr. Donald C. Matthews, Dept. of Zoology and Entomology, University of Hawaii, for his kind help in correcting this paper, and for the valuable suggestions made.

Summary

1. When *Aplysia juliana* Pease is kept up till 6 hours in 80% sea water, it shows an increase in oxygen consumption of about 438%, as compared with the normal respiration, during the first 30 minutes. After this time it decreases rapidly at first, more slowly later. When transferred to 100% sea water after a stay of about 6 hours in diluted sea water, the oxygen consumption continues to decrease. The weight- and blood-salinity curves show a course more or less comparable to those found by Bethe in *Aplysia*. However, since the animals do not recover in 100% sea water after being subjected to 80% sea water for 6 hours, it is concluded that the results obtained are those from irreparably damaged animals and hence conclusions as to osmoadjustment or osmoregulation cannot be drawn.

2. The same experiments performed with animals subjected to a stay in 95% sea water, show that here there occurs a definite, be it rather weak, osmoregulation. *Aplysia juliana* is therefore certainly not a "pure" osmoadjustor.

3. Review of the pertinent literature shows that (weak) osmoregulation seems to be more wide-spread in marine molluscs than was thought to be.

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Primary Organic Productivity of a Hawaiian Coral Reef[1]

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ABSTRACT

Primary organic productivity was determined by measuring changes in oxygen concentration of sea water flowing over a fringing coral reef at Kapaa, Kauai, Hawaii. Prevalence of a rather strong, unidirectional current facilitated use of this method.

Determinations were made both in summer (July) and winter (November). The reef is autotrophic, as were two previously studied atoll reefs in the Marshall Islands. Gross primary productivity is about 2,900 g C/m²/yr. This is in impressive agreement with results obtained on the atoll reefs, which are the only previous measurements of coral reef productivity.

All three results are considerably higher than determinations of productivity of open ocean waters. The authors attribute this difference to photosynthesis by benthic algae on the coral reef platform.

INTRODUCTION

The attention of many oceanographers has in recent years been directed toward measurement of rates of biological productivity of the oceans. Riley (1941) summarized data available at that time, most of which had been obtained from the North Atlantic Ocean. More recently, studies of primary organic productivity have been extended to other parts of the open ocean (Steemann Nielsen 1952, 1954, and others; see also Fleming and Laevastu 1956) and to coral reefs.

Prior to the investigation reported in this paper, the only definitive data on coral reef productivity were those provided by Sargent and Austin (1949, 1954) and Odum and Odum (1955) for atoll reefs in the Marshall Islands.

The present paper provides comparable data for a fringing reef in the Hawaiian Islands. It will be shown that (1) the rate of organic production on the reef is sufficient to meet the needs of the consumer organisms present, and (2) the rate of gross primary productivity is of the same order of magnitude as those reported in the two Marshall Islands studies. These rates are considerably higher than those reported for open oceans and, with one exception, somewhat higher than those reported for even the most productive coastal waters. An explanation is advanced to account for this discrepancy.

Location and description of the reef

The investigation was carried out on North Kapaa Reef, at Kapaa, on the windward (east) coast of the island of Kauai (Fig. 1). The reef was visited in October and November of 1955, and in July, 1956.

North Kapaa Reef extends for about 4,000 feet fringing an approximately north-south shoreline (Fig. 2). Its southern boundary is a small stream and stone jetty. A small embayment of deep water which approaches a steeply sloping shore marks its northern limit. The reef reaches a maximum width of 1,400 feet near its southern end and gradually narrows to 500 feet at the northern end.

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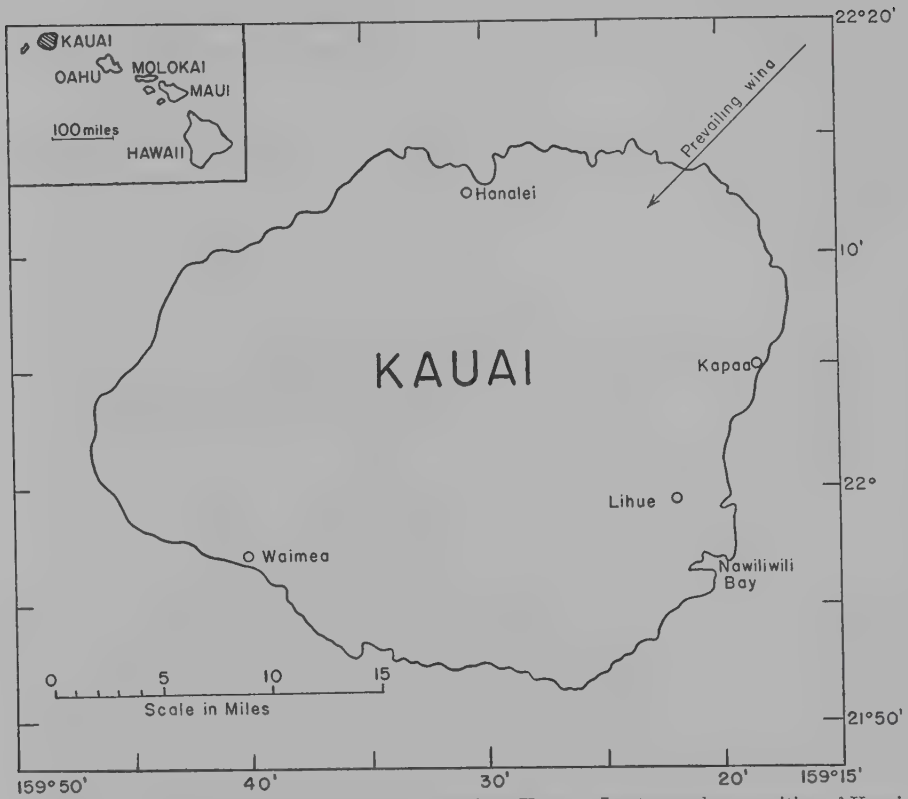

FIG. 1. Outline map of Kauai. The reef studied is at Kapaa. Inset map shows position of Kauai (hatched) in the Hawaiian Islands.

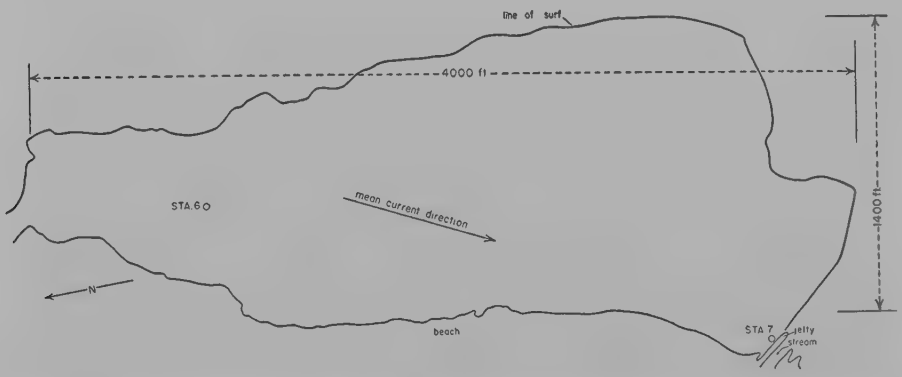

FIG. 2. Outline map of North Kapaa Reef, showing stations, mean current direction, and important topographic features.

Depth of water over the reef varies from 6 to 173 cm above mean sea level. Mean depth was calculated to be 79 cm. This datum represents the average of 107 measurements of depth with respect to mean sea level made by the Lihue Plantation Co., Ltd.

The substratum is characterized by irregular areas of living and dead coral, coral rubble, and sand. The distribution and abundance of benthic organisms vary with the nature of the substratum. A detailed survey of the flora and fauna was not made; however, the general distribution and abundance of prominent organisms were noted (Helfrich and Kohn 1955). Benthic algae, which are of special interest, are represented chiefly by the genera *Acanthophora*, *Lyngbya*, and *Padina*. Other genera of large plants present are *Ulva*, *Halimeda*, *Sargassum*, and *Amansia*. The encrusting *Porolithon*, *Goniolithon*, and *Lithothamnion* occur especially toward the seaward edge of the reef.

Investigations of currents over the reef revealed a definite pattern. A rather strong, unidirectional current prevails. Fifty-two determinations in October and November of 1955 gave a mean current velocity of 24 cm/sec and a mean heading of 220°T. Twenty determinations in July, 1956, gave a mean velocity of 22 cm/sec and a mean heading of 218°T. The current is thus approximately parallel to the coastline and to the prevailing northeast trade winds. At the southern end of the reef the current is deflected out to sea by the jetty (Fig. 2) and reached a maximum velocity of 44 cm/sec. (Measurements of currents at this station [Sta. 7] were not included in average velocities and headings.)

Vertical diurnal tide range is only about 1.8 feet in the area under consideration. Calculations made for the authors by D. C. Cox, Senior Geologist, Hawaiian Sugar Planters Experiment Station, showed that the volume of water moved on and off the reef with change in tidal phase does not cause a significant tidal current. This was verified by plotting observed current velocities against time and tidal phase (Fig. 3). These graphs show significant increases in mean

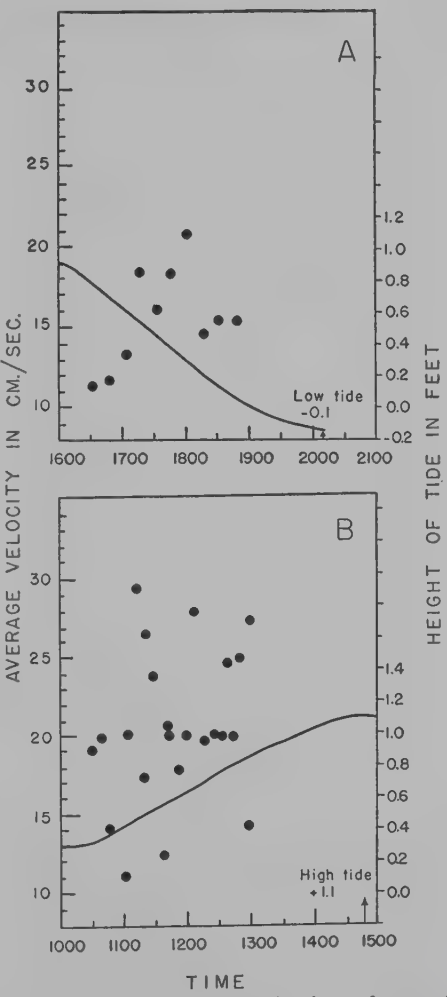

FIG. 3. Individual determinations of current velocity (●), and height of tide (——), plotted against time of day, showing absence of relationship between current velocity and phase of tide. *A*, 29 October 1955. *B*, 30 October 1955.

current velocity with time; however, it should be noted that the determinations on 29 October were made while the tide was falling, while those on 30 October were made during rising tide.

METHODS

Two stations (Sta. 6 and 7) were established on the reef such that a line drawn

between them was approximately parallel to the mean current direction (Fig. 2). Distance between the stations was 861 meters.

Each of the determinations of current velocity cited above consisted of recording the time required for a fluorescein dye spot to travel a distance of 5 m. Current direction was determined by sighting with a compass from the point of release of the dye spot to its position after traveling 5 m.

Water samples were collected in 300-ml glass-stoppered bottles at intervals over a 24-hour period. Samples were taken at a depth of approximately six inches below the surface. They were fixed immediately for determination of dissolved oxygen by the Winkler method. The samples were kept in darkness and titrated upon return to the laboratory 2–3 days later. Replicate samples of 50 ml were titrated with 0.01 N sodium thiosulfate standardized with potassium biniodate (Harleco).

In the November series, records for a single cycle were obtained. In July, data were obtained for two successive 24-hour cycles.

Water temperature at each station (Fig. 4A) and incident light intensity (Fig. 4B) were measured simultaneously with collection of each water sample in the July series. A Norwood Director exposure meter placed on a level surface on the shore near Sta. 7 was used to measure incident light. At times of intermittent cloudiness series of readings were taken and averaged. Meter readings were converted to foot-candles by multiplication by the appropriate factor. Data on cloud cover (Fig. 4B, 5A) as well as other weather data were obtained from the Weather Bureau Pacific Supervisory Office in Honolulu, through the courtesy of D. I. Blumenstock. All Weather Bureau observations were made at Lihue, Kauai, approximately ten miles south of Kapaa.

RESULTS

Observations of 27–29 July 1956

In the July series of observations an effort was made to test the methods used by comparison of productivity during two successive 24-hour cycles. The results are summarized in Figure 4. Water temperature fluctuated diurnally at both the upstream station (Sta. 6) and the downstream station (Sta. 7), as shown in Figure 4A. Maximum and minimum temperatures and diurnal ranges at both stations are given in Table 1. The greater amplitude of fluctuation at Sta. 7 is attributed to the increased surface/volume ratio of the water as it flows from the open ocean across the shallow reef platform.

Measurements of incident light and the extent of cloud cover are shown in Figure 4B.

Results of oxygen determinations at each station are shown graphically in Figure 4C. At both stations a diurnal cycle of oxygen concentration is apparent. The greater amplitude at Sta. 7 is attributed to biological activity on the reef platform.

The mean observed current velocity in July was 22 cm/sec. The time required for water to pass from Sta. 6 to Sta. 7 was close to one hour (3910 sec.). Therefore, the curve for Sta. 6 in Figure 4C has been shifted to the left by one hour, according to the convention suggested by Odum (1956). This enabled analysis of the data in such a way as to make possible the determination of rates of primary organic production (photosynthesis) and consumption (respiration) on the reef. This method was first used by Sargent and Austin (1949, 1954).

Since the mean compass bearing of Sta. 7 from Sta. 6 was 218°T. and the mean current direction was 220°T., the two stations utilized were virtually on a line coinciding with the mean current direction, and no correction for angle of current was necessary.

The mean rate of change of oxygen concentration in milliliters per centimeter of reef normal to the current (*i.e.* in a strip 1 cm wide between the two stations) is given by the formula

$$\text{mean depth (cm)} \times \text{velocity (cm/sec)} \times \text{mean change in oxygen between stations (ml/cm}^3\text{)} = \text{mean change in oxygen over reef (ml/cm/sec)} \quad (1)$$

Substitution in Equation (1) of observed values for mean depth and mean current velocity gives

$$79 \times 22 \times (\text{ml/L}_{\text{Sta. 7}} - \text{ml/L}_{\text{Sta. 6}}) \times 10^{-3} = \text{ml/cm/sec}. \quad (2)$$

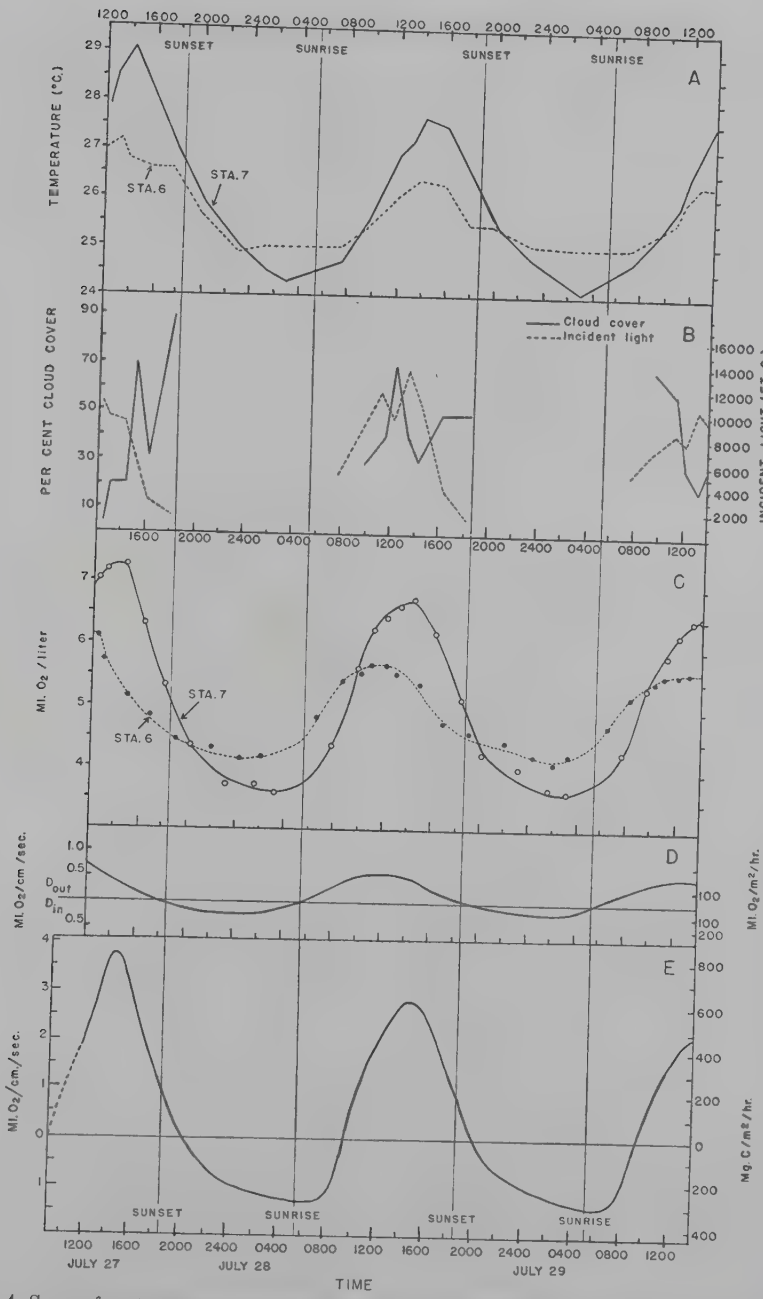

FIG. 4. *A*, Sea surface temperatures at Sta. 6 and 7. *B*, Incident light and cloud cover. *C*, Oxygen concentration at Sta. 6 and 7. *D*, Diffusion of oxygen across the air-sea interface. *E*, Production and consumption of organic matter. Data from North Kapaa Reef, 27–29 July 1956.

TABLE 1. *Temperature (°C) maxima, minima, and ranges at stations 6 (upstream) and 7 (downstream)*

	Maximum		Minimum		Range	
	Sta. 6	Sta. 7	Sta. 6	Sta. 7	Sta. 6	Sta. 7
27–28 July	27.2	29.1	24.9	24.3	2.3	4.8
28–29 July	26.4	27.1	25.0	24.1	1.4	3.0

As emphasized by Odum (1956) the curve of this equation is not equivalent to the difference between rates of gross primary productivity and respiration but includes also the result of exchange of oxygen with air.

A convenient method of correcting for diffusion of oxygen across the air-sea interface is presented by Odum (1956) in the following equations:

$$D = KS \tag{3}$$

where D is the diffusion rate per area, K is the gas transfer coefficient defined on an area basis, and S is the saturation deficit between water and air.

$$K = \frac{z(q_m - q_e)}{S_m - S_e} \tag{4}$$

where z is the mean depth, q_m is the rate of change of oxygen concentration before sunrise, q_e is the rate of change of oxygen concentration after sunset, S_m is the saturation deficit before sunrise, and S_e is the saturation deficit after sunset. Since respiration is assumed to be constant it does not affect q.

The gas transfer coefficient K is also known as the invasion coefficient (Dorsey 1940), and the exchange coefficient, E (Redfield 1948). The only values which have been calculated for the oceans are those given by Redfield (1948) for the Gulf of Maine. The coefficient in winter was 13×10^6, and in summer, 2.8×10^6 ml $O_2/m^2/month/atmosphere$. The value calculated for North Kapaa Reef is 3.3×10^6 ml $O_2/m^2/month/atmosphere$. Redfield's calculations were based on saturation values given by Fox (1909), which have since been superseded by those of Truesdale, Downing, and Lowden (1955). Use of the data of Fox's tables in the calculation for North Kapaa Reef would increase K by about 15%.

In order to plot the diffusion curve (Fig. 4D) in the same units as Equation (2), z is in meters, q_m and q_e in $ml/m^2/hr$, and S_m and S_e are expressed as the head of oxygen pressure across the sea surface, in atmospheres, calculated from the formula given by Redfield (1948: p. 355) using the saturation data of Truesdale, Downing, and Lowden (1955). Thus K may be expressed in ml/cm/sec/atm. Since S, like S_m and S_e, is in atm, D is in ml/cm/sec. The cm in this expression, as in Equations (1) and (2), refers to a strip of reef 1 cm wide between the two stations, which is equivalent to an area of 8.6 m^2. Diffusion may thus be converted to an areal basis, as has been done on the right ordinate of Figure 4D.

The curve of Equation (1) corrected for diffusion by algebraic addition of the diffusion curve (Fig. 4D) is plotted as Figure 4E. The portion of the curve above the zero or compensation line represents an excess of primary organic production over consumption. The portion below the line represents net consumption.

The nocturnal level of respiration is of interest. The difference between stations during the night decreases to a minimum of about -1.4 ml $O_2/cm/sec$ near sunrise (or shortly after, suggesting a lag). This represents nocturnal respiration by all of the organisms on the reef, and it may be used as an indication of respiration of the entire biological community on the reef. The area of a rectangle bounded by 0 and -1.4 ml $O_2/cm/sec$ on the ordinate of Figure 4E and extending for 24 hours on the abscissa is equivalent to 121,000 ml of oxygen consumed per cm (= 8.6 m^2) per 24-hour day, or 14,100 $ml/m^2/day$.

Since clear evidence to the contrary is lacking, it is simplest to assume that the rate of plant respiration is independent of the rate of photosynthesis (Odum 1956, Ryther 1954). Therefore, the consumption of 14,100 ml of oxygen per square meter per day may be taken as the respiration rate of the entire community, and it reflects quantitatively the biomass present. This datum is introduced here with the suggestion of possible future correlations between measurements of biomass and rates of metabolism of biological communities.

TABLE 2. *Net production and consumption in ml O_2/cm on North Kapaa Reef, 27–29 July 1956*

Based on graphical integration of areas above (production) and below (consumption) 0-line in Figure 4E.

	Net production	Net consumption
27–28 July	73,700	45,600
28–29 July	64,600	46,700

In order to compare net production and consumption on the reef, the curve of Figure 4E was graphically integrated. Values for net production (area above 0 line) and net consumption (area below 0 line) are given for the two days studied in Table 2. Inspection of Table 2 and Figure 4E shows reasonable similarity of the data for successive days, thus affirming the validity of the method. The first sample collected was at 1200 on 27 July. In order to obtain a complete cycle for this date, the time of the 0 intercept was taken as the average (0916) of the observed times on 28 July (0920) and 29 July (0912). For this reason, the portion of the curve for 27 July between 0916 and 1200 is shown as a dotted line in Figure 4E. Mean net production was about 69,200 ml and mean net consumption about 46,600 ml of oxygen for a 24-hour day. There is thus a mean excess of 22,600 ml of oxygen per day.

The rate of primary production of living substance is of greater interest than the rate of exchange of oxygen *per se*. Therefore, in the conversion to areal units on the right ordinate of Figure 4E, milliliters of oxygen have been converted to milligrams of carbon by the simplified photosynthesis equation,

$$CO_2 + H_2O = (CH_2O) + O_2 \qquad (5)$$

The daily excess of 22,600 ml of oxygen is equivalent to 12,100 mg of carbon, by which production exceeds consumption per centimeter of reef normal to the current per day. In areal units, the excess is about 1,400 mg C/m²/day.

Production averaged 4,300, and consumption 2,900 mg C/m²/day, giving the production excess of 1,400 mg C/m²/day. In summer, a significantly greater amount of organic matter is thus produced on the reef over that which is consumed. Thus, the reef is self-sufficient, or autotrophic, at least during this part of the year. The excess is presumably stored on the reef as organic biomass.

In order to determine gross primary productivity, the entire curve (Fig. 4E) above the baseline (−1.4 ml O_2/cm/sec) was graphically integrated. This represents 133,000 ml O_2/cm/day for the only complete cycle covered by the observations (28 July). This is equivalent to about 71.3 g C/cm/day, or 8.3 g C/m²/day. The ratio of gross primary productivity to community respiration (P/R) is 1.1.

If this rate of production were maintained throughout the year, annual productivity would be 3,000 g C/m².

Observations of 25 November 1955

The results of the initial study, made 25 November 1955, are summarized in Figure 5. Temperature measurements taken at this time were too few to permit construction of curves of diurnal fluctuation and diffusion. Those obtained were about 1.5°C lower than corresponding values in July.

Incident light measurements were not made in the November series, but the extent of cloud cover for the period under consideration has been plotted in Figure 5A. In the field notes it was stated that the "data were collected on a day throughout which the sun shone brightly."

Results of determinations of oxygen concentrations at each station are shown graphically in Figure 5B. The diurnal cycle at both stations is apparent, as is the greater amplitude of the curve for Sta. 7, which is expected from increased biological activity on the reef platform.

The mean observed current velocity in November was 24 cm/sec. Time required for water to pass from Sta. 6 to Sta. 7 was one hour (3590 sec). Therefore, the curve for Sta. 6 in Figure 5B has been shifted to the left one hour. Since the mean current direction was close to the compass bearing of Sta. 7 from Sta. 6, correction for angle of current was not necessary.

The rate of change in oxygen concentra-

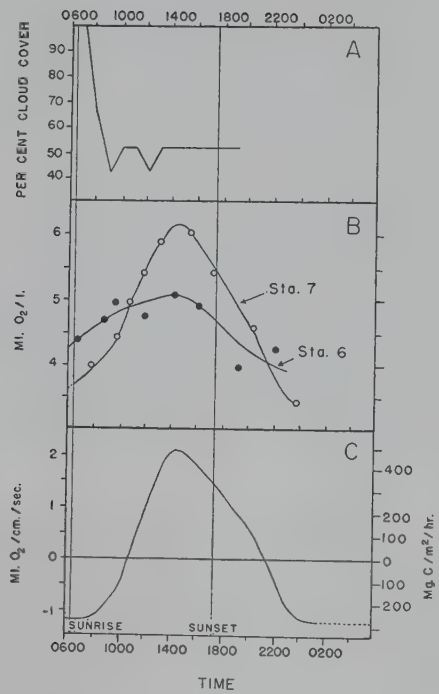

FIG. *A*, Cloud cover. *B*, Oxygen concentration at Sta. 6 and 7. *C*, Production and consumption of organic matter (not corrected for diffusion). Data for North Kapaa Reef, 25 November 1955.

tion between stations throughout the 24-hour cycle is plotted in Figure 5C. This graph is not directly comparable with Figure 4E, since the latter has been corrected for diurnal fluctuation of diffusion, while the former has not.

The nocturnal level of respiration in Figure 5C is about −1.2 ml/cm/sec. Since diffusion is in the direction of air to water at night, its effect is to reduce the apparent difference in concentration between Sta. 6 and Sta. 7. Thus the observed rate of respiration is probably too small. The actual rate probably approaches closely the July rate of −1.4 ml/cm/sec, or consumption of 14,100 ml/m²/day.

Graphic integration of the curve (Fig. 5C) gives uncorrected values of 47,100 ml O_2/cm/sec net production and 46,900 ml O_2/cm/sec net consumption. In the July series of observations, correction for diffusion resulted in increasing net productivity by 20.7% and increasing net consumption by 11.5%. If this discrepancy applies also in winter, daily production is probably somewhat greater than daily consumption. Thus in winter as well as in summer, sufficient organic matter is produced on the reef to meet the demands of the consumer organisms present.

Gross productivity, as calculated from the uncorrected curve (Fig. 5C) is 103,100 ml O_2/cm/day. In the July series, correction for diffusion raised the calculated gross productivity by 19.5%. Application of this factor to the November result gives a corrected gross productivity of 123,200 ml O_2/cm/day. This is equivalent to 7.7 g C/m²/day, somewhat lower than the 8.3 g/m²/day for July.

If the calculated summer and winter values are each assigned one-half year, annual gross primary productivity is calculated to be 2,900 g C/m².

Efficiency of gross production

Determinations of solar radiation made by the writers were not sufficiently numerous to support an estimate of photosynthetic efficiency. Records of insolation obtained at the Hawaiian Sugar Planters Association Experiment Station in Honolulu indicated 7.15×10^6 cal/m²/day for 30 July 1956. Using the energy equivalent of the July production datum of 8.3 g C/m²/day, efficiency of gross productivity was calculated to be 1.1%. This is lower than the value of 5.8% measured on an atoll reef (Odum and Odum 1955) but somewhat higher than other marine communities. Riley (1941) calculated values of 0.55–0.82% efficiency for phytoplankton in Long Island Sound.

DISCUSSION

In previous quantitative determinations of primary productivity of coral reefs, no corrections for diffusion of oxygen have been made. For this reason, the directly comparable uncorrected curve for North Kapaa Reef are shown in Figure 6. In Figure 6A,

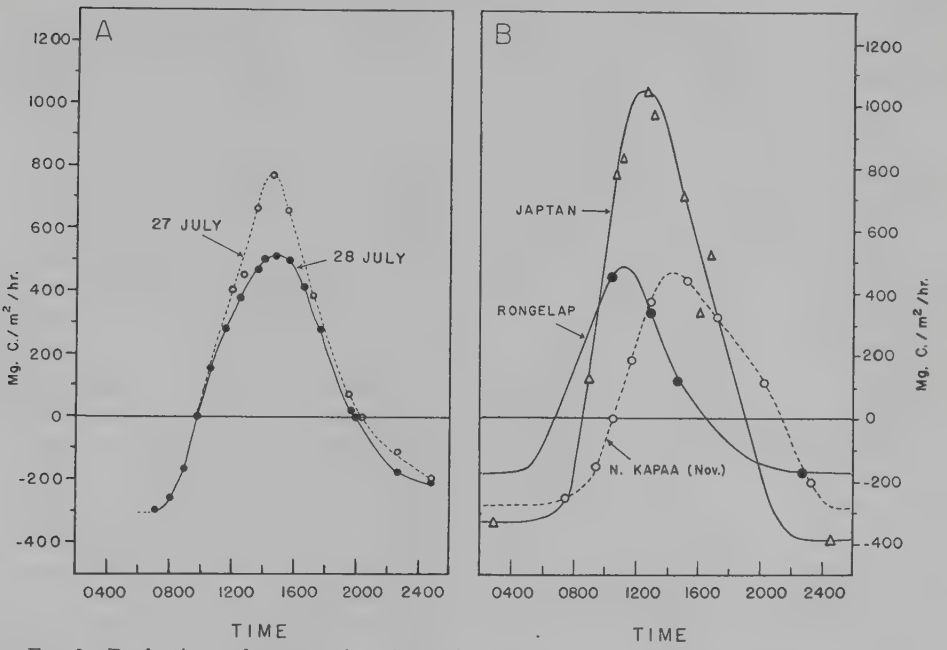

FIG. 6. Production and consumption of organic matter. *A*, North Kapaa Reef, 27 July 1956 and 28 July 1956. *B*, North Kapaa Reef, 25 November 1955; reef at Japtan Island, Eniwetok Atoll; and reef at Bokujarito Island, Rongelap Atoll. Data not corrected for diffusion. Data from Japtan and Bokujarito are from Odum and Odum (1955) and Sargent and Austin (1954), respectively.

the two cycles observed on North Kapaa Reef in July have been superimposed to facilitate comparison. The curves obtained by Sargent and Austin (1949, 1954), Odum and Odum (1955), and for North Kapaa Reef in November have been recalculated in terms of mg C/m²/hr and included in Figure 6B.

It is noteworthy that the peaks of production for the three determinations made on North Kapaa Reef (27 and 28 July and 25 November) are in very close agreement. All three fall between 1400 and 1430. They are later, however, than those obtained by Sargent and Austin (1949, 1954) at Rongelap (before noon) and by Odum and Odum (1955) at Japtan (about 1230). Sargent and Austin (1954) point out that a morning peak is reasonable in the light of results obtained by Kostytschew *et al.* (1926, 1930), who observed that the rate of photosynthesis both in land and water plants reached a maximum before noon and then declined. Yonge, Yonge, and Nichols (1932) also observed this phenomenon in reef corals.

Odum and Odum (1955) explain that the lag between sunlight intensity and oxygen production may be partially due to location of photosynthesizing organisms beneath the surface of the calcareous reef surface, sand, and coral polyps. This also seems the best explanation for the occurrence of a lag in peak production at North Kapaa Reef. However, it does not explain why the peak at Kapaa is later than at Japtan. The discrepancies in time of peak production in these investigations seems sufficient to suggest that this aspect requires further investigation, especially with regard to the extend of oxygen production and its rate of diffusion from primary producers within coral and other types of substratum.

The three coral reefs that have been studied all show a daily excess of production of organic matter over consumption.

TABLE 3. *Gross primary organic productivity of marine environments*

Location	Gross productivity g C/m²/yr	Reference
Coral Reefs		
Rongelap Atoll, Marshall Is.	1500 (1800)[1]	Sargent and Austin (1954)
Eniwetok Atoll, Marshall Is.	3500 (4200)[1]	Odum and Odum (1955)
North Kapaa Reef, Kauai, Hawaii	2900	Present paper
Turtle Grass Bed		
Long Key, Florida	4650	Odum (1956)
Open Ocean		
Off Rongelap Atoll, Marshall Is.	28	Sargent and Austin (1954)
Off Hawaii	37	Steemann Nielsen (1954)
Off Hawaii[2]	21	Doty and Oguri (1956)
Off Hawaii (Inshore waters)[3]	123	Doty and Oguri (1956)
Sargasso Sea	167	Riley, Stommel, & Bumpus (1949)
Georges Bank	309	Riley, Stommel, & Bumpus (1949)
Long Island Sound	470	Riley (1956)
Benguela Current	167–912	Steeman Nielsen (1954)

[1] With estimated correction for diffusion.
[2] Average of Stations 1 and 2.
[3] Station 3.

Sargent and Austin (1954) reported net production of 0.5 g C/m²/day, and Odum and Odum (1955) 9 g C/m²/day. The mean net production in the present study, corrected for diffusion, is 7.9 g C/m²/day.

In the second column of Table 3, the annual values of gross productivity reported by Sargent and Austin (1954) and Odum and Odum (1955) are listed. These values were not corrected for diffusion. For North Kapaa Reef, the diffusion correction represents an increase of 19.5%. This factor has been applied to the Marshall Islands data to give an estimate of corrected gross productivity. These values are placed in parentheses in Table 3.

Two important aspects of these data merit further discussion. First, the present authors are impressed by the fact that all three of the coral reefs thus far studied show gross productivity values of the same order of magnitude, when determined by the flow method. The highest value differs from the lowest by a factor of about two. Sargent and Austin (1954) described the reef at Rongelap as appearing "rather barren of plants." The rich biota of Japtan Reef, Eniwetok Atoll, is described in detail by Odum and Odum (1955). Standing crop on North Kapaa Reef, although not quantitatively determined, may well lie in between the other two reefs.

Second, these values are one to two orders of magnitude greater than those reported for almost all other marine environments. Data from other areas are included for comparison in Table 3. Excluding the coral reef and turtle grass communities, the highest values are for Long Island Sound, a shallow, protected body of water characterized by a nutrient-rich, freshened surface layer, and for the southern part of the Benguela current. The latter is a locality of marked upwelling. A single experiment gave a rate equivalent to 1387 g C/m²/yr, but considerable variation was expected (Steemann Nielsen 1954). In all of the other regions cited, with the probable exception of Doty and Oguri's (1956) Sta. 3, the base of the euphotic zone is above the ocean floor. In contrast, the shallow coral reef platforms support more or less dense populations of benthic algae. Productivity due to phytoplankton of neighboring oceanic water is extremely low. It is apparent that the extremely high gross primary productivity of coral reefs is attributable to photosynthesis by benthic algae on the reef platforms.

The extensive substrate area covered by a shallow layer of constantly flowing sea water is concluded to be the major factor responsible for the productivity of coral reefs being two orders of magnitude higher than adjacent oceanic waters. The substrate enables the growth of large attached algae, as well as algae which live within the substratum in a strongly illuminated region of the sea. In some regions, attached phanerogams play an important role. The strong constant flow of water provides these plants with a continual source of nutrients. The plants in turn promote a rich community of large and small animals confined to the same surface. Communities of adjacent areas may also benefit, as indicated by higher phytoplankton productivity of Hawaiian inshore waters (Doty and Oguri 1956).

The highest gross primary productivity

value reported for a marine community is 4650 g C/m²/yr (Odum 1956). It was obtained at a depth of three feet in a bed of turtle grass (*Thalassia*), which is undoubtedly the primary source of this productivity.

SUMMARY

Primary organic productivity was determined by measuring changes in oxygen concentration of sea water flowing over a coral reef at Kapaa, Kauai, Hawaii. Prevalence of a rather strong, unidirectional current facilitated use of this method. Determinations were made both in summer (July) and in winter (November).

The reef is autotrophic, that is the rate of organic production is sufficient to meet the requirements of the consumer organisms present. This was also found to be the case on two atoll reefs in the Marshall Islands, on which studies of this type had previously been made.

Gross primary productivity was calculated to be 2,900 g C/m²/yr. This is in impressive agreement with data obtained by Sargent and Austin (1954) and Odum and Odum (1955) on the atoll reefs.

The ratio of gross productivity to community respiration was calculated to be 1.1. Efficiency of gross productivity was calculated to be 1.1%.

Except for a rather specialized turtle grass community, the primary productivity of coral reefs is far greater, on an areal basis, than all other marine environments that have been studied. The authors attribute this difference to photosynthesis by benthic algae on the reef platforms.

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Further Evidences of Anomuran Non-pedunculate Spermatophores[1]

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Further Evidences of Anomuran Non-pedunculate Spermatophores[1]

DONALD C. MATTHEWS[2]

MACRURAN NON-PEDUNCULATE SPERMATOPHORES were differentiated from anomuran pedunculate spermatophores by Calman (1909), but subsequent studies embracing both macrura of the Palinuridae, Scyllaridae, and Nephropsidae (Matthews, 1951, 1954*b*, 1954*c*) and the anomura of the Paguridae (Mouchet, 1931; Matthews, 1953, 1956), placed this differentiation in doubt. However, not until it was discovered that a macruran, *Parribacus antarcticus*, elaborated pedunculate spermatophores (Matthews, 1954*a*) and an anomuran, *Hippa pacifica*, elaborated non-pedunculate spermatophores (Matthews, 1956) was the dichotomy between these two tribes proven to be untenable.

This paper, which compares the development of *Aniculus maximus* spermatophores with that of certain other Paguridae, records still other instances in which anomuran non-pedunculate spermatophores are produced.

MATERIALS AND TECHNIQUES

Mature specimens of *Aniculus strigatus* Herbst (Edmondson, 1946: 264; Forest, 1952: 19, *Trizopagurus strigatus* (Herbst)), collected at Hanauma Bay, Oahu, T. H., during the year 1954, and of *A. maximus* (*vide* Edmondson, *opus cit.* p. 79), obtained from the Honolulu Aquarium during the year 1953, were used in this study.

The right testis and vas deferens of each specimen of *A. maximus* were fixed either in Bouin's or Zenker's fluid, dehydrated and cleared in dioxane, embedded in Tissuemat (54–56°C.), and serially sectioned at 10 microns. The mounted sections were stained either with Harris's alumhaematoxylin (counterstained with eosin) or with Mallory's Triple Stain.

The left vasa deferentia of both species were immersed for 10–30 minutes in an aqueous solution of toluidine blue (1–10,000), teased open in sea water, and their vitally stained spermatophores studied.

OBSERVATIONS

In cross sections throughout the testis of *A. maximus* immature sacculi containing primary spermatocytes, and more mature sacculi containing secondary spermatocytes and spermatids, are observed. These sacculi, by the renewed activity of their germinal epithelial cells, produce new primary spermatocytes which, as they fill the sacculi, force the metamorphosing spermatids into the minute collecting tubule. Thus by combined, rhythmical activities of numerous sacculi a continuous sperm mass slowly enters the proximal portion of the vas deferens where, molded in compliance with the circular lumen, it forms a rodlike sperm column.

Serial cross sections through this region of the vas deferens disclose that the shape of the lumen gradually changes from circular to elliptical, synchronously effecting corresponding changes in the shape of the sperm column.

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As the sperm column becomes elliptical, a secretion from the epithelial cells bounding the more pointed extremities of the elliptical lumen envelops the sperm column and forms the sperm column sheath.

Serial sections through somewhat more distal regions of the vas deferens disclose that the lumen gradually becomes pear-shaped. In longitudinal sections through this region (Fig. 1) the sheathed, sperm column appears as a series of partially closed arches (*c*), joined one to another by portions of the compressed, empty, sperm column sheath (*d*).

Longitudinal sections through slightly more distal regions of the vas deferens (Fig. 2) disclose that a secretion from the epithelial cells (*f*) bordering the narrow portion of the lumen forms the foot (*e*) and fills with precursory stalk material (*d*) the spaces between the closing arches.

Thus far, the histological and physiological phenomena of spermatophoric development in *A. maximus* parallel those of *Dardanus punctulatus* (Matthews, 1956) and *Dardanus asper* (Matthews, 1953: 260–262, figs. 7, 8, 9, 10, 11) in which truly pedunculate spermatophores are ultimately elaborated.

In *D. asper*, as in *A. maximus*, the living vasa deferentia exhibit spasmodic contractions which serve both to move the sperm mass and to mold it in compliance with the gradually changing internal die, i.e., first cylindrical, then elliptical, then pear-shaped. In *D. asper* also, a secretion from epithelial cells isolated at opposite ends of the elliptical lumen forms the sperm column sheath. And this sheathed sperm column, by muscular contractions of the wall of the vas deferens, forms partially closed arches, joined one to another by portions of the compressed, empty, sperm column sheath. In *D. asper*, too, a secretion from the epithelial cells bordering the narrow portion of the pear-shaped lumen forms the foot and fills with precursory stalk material the spaces between the closing arches.

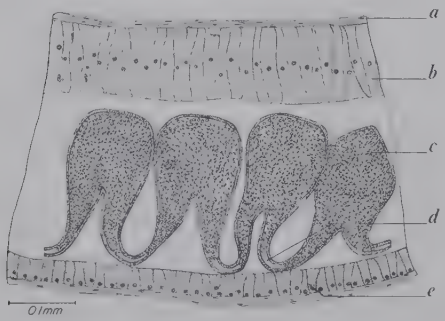

FIG. 1. Longitudinal section of the proximal vas deferens of *Aniculus maximus* showing: *a*, muscle layer; *b*, elongate epithelial cells; *c*, partially closed arches of sheathed, sperm column; *d*, compressed, empty sperm column sheath connecting partially closed arches; *e*, short, epithelial cells bounding narrow portion of lumen.

From this stage of development on, the processes in the elaboration of pedunculate and non-pedunculate spermotophores diverge. This divergence results, for the most part, from subsequent activities of the epithelial cells bounding the lumen.

In *D. asper* (*op. cit.*, p. 263, figs. 12, 13), the epithelial cells at the narrow region of the pear-shaped lumen form a groove into which the precursor of the stalks is secreted. As the groove deepens, the stalk material lengthens both by the continued secretion of the epithelial cells and by the muscular contractions in the walls of the vas deferens. It is noteworthy that the lengthening of the stalks carries the ampullae of sperm "above" the foot and that the connecting sperm column sheaths between adjacent ampullae become extremely thin and finally obscure. Even in the short spermatophores of *Birgus latro* and *Coenobita rugosus* (Matthews, 1956) the stalks are lengthened sufficiently to carry the ampullae of sperm "above" the foot.

In *A. maximus* (Fig. 3) the epithelial cells (*f*) fail to form a deep groove into which the precursor of the stalks is secreted. Instead, this region of the lumen (*d*) widens and the secretion from the epithelial cells spreads out forming the broad foot (*e*). Noteworthy also is the sectioned portion of an arch (*c*), which here measures 112 microns high and 71 mi-

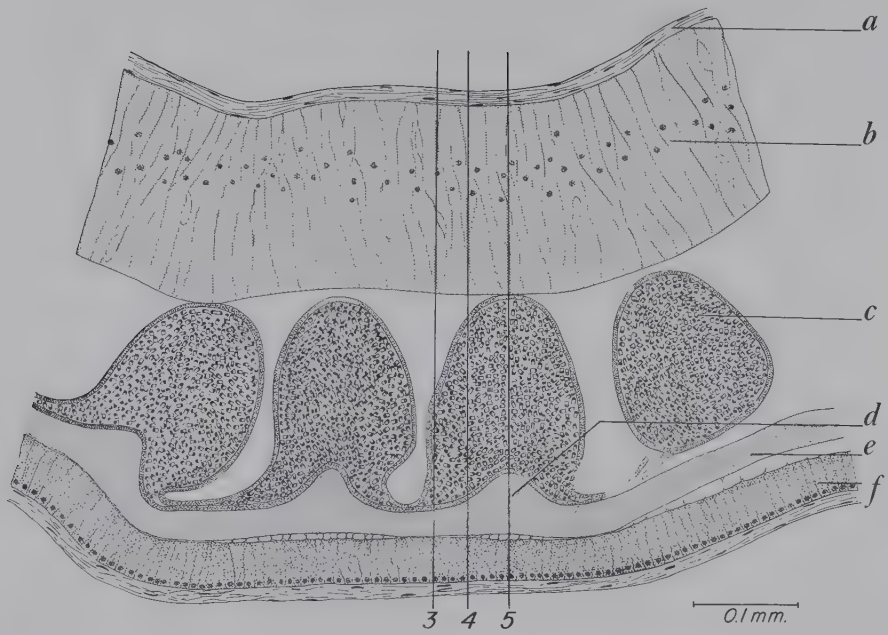

FIG. 2. Longitudinal section of the proximal vas deferens of *Aniculus maximus* (slightly distal to Fig. 1) showing: *a*, muscle layer; *b*, elongate epithelial cells; *c*, sectioned portion of arch; *d*, precursory stalk material; *e*, foot; *f*, short epithelial cells of narrow portion of lumen secreting the foot material. (The numbers 3, 4, 5 show regions through which Figs. 3, 4, 5 are taken.)

crons wide and appears like a distinct ampulla resting on the broad foot (*e*).

In subsequent sections through this region of the vas deferens (Fig. 4) although the foot forming epithelial cells (*f*) do not shorten, the epithelial cells (*b*) "above" the sectioned portion of the arch (*c*) attain a length of approximately 182 microns. Again it is noteworthy that the sectioned portion of the arch (*c*) appears like a distinct ampulla 171 microns high and 118 microns wide. Whereas, in Figure 3 the "ampulla" appeared to rest firmly on the broad, basal foot, in Figure 4 it is "elevated" approximately 12 microns by the sectioned portion of the stalk precursor (*d*).

In still other cross sections through this region of the vas deferens (Fig. 5) neither the foot forming epithelial cells (*f*) nor the epithelial cells (*b*) above the sectioned portion of the arch (*c*) change appreciably in length. And again it is noteworthy that the sectioned portion of the arch (*c*) appears like a distinct ampulla, 171 microns high and 118 microns wide. The "ampulla" is elevated approximately 35 microns above the foot (*e*) by the sectioned portion of the stalk precursor (*d*).

The broad groove so characteristic of this portion of the lumen is no longer encountered in cross sections through the enlarged, apical portion of the vas deferens (Fig. 6). Gradually, the epithelium becomes folded and two typhlosole-like regions (*b*) appear at opposite sides of the lumen. From the epithelial cells bordering the crypts of these typhlosole-like folds, a new mucus-like secretion forms the matrix (*c*) which encompasses the completed spermatophores.

Because of its tortuous nature, both cross sections (*e*) and longitudinal sections (*d*) of

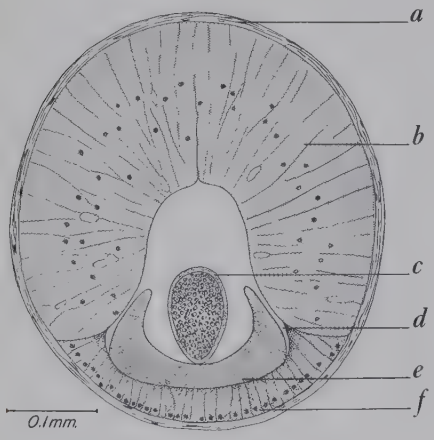

FIG. 3. Cross section of the proximal vas deferens of *Aniculus maximus* (through region 3 of Fig. 2) showing: *a*, muscle layer; *b*, elongate epithelial cells; *c*, sectioned portion of arch; *d*, portion of wide lumen; *e*, foot; *f*, foot-forming epithelial cells.

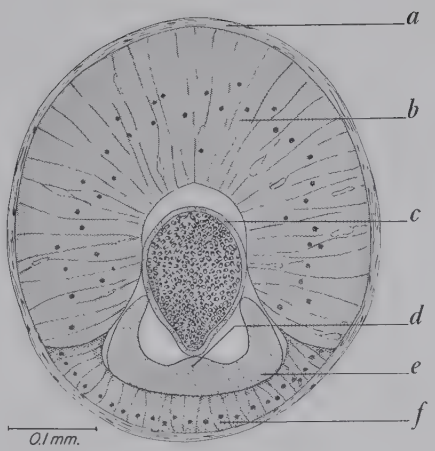

FIG. 4. Cross section of the proximal vas deferens of *Aniculus maximus* (through region 4 of Fig. 2) showing: *a*, muscle layer; *b*, elongate epithelial cells; *c*, sectioned portion of arch; *d*, stalk precursor; *e*, foot; *f*, foot-forming epithelial cells.

the spermatophore are here observed. Conspicuous also in these sections are the longitudinal muscles (*a*) which probably serve to eject the completed spermatophores (Fig. 7).

When the enlarged apical portions of the vasa deferentia of *A. strigatus* and *A. maximus* are placed in toluidine blue and their encompassing mucus-like matrices are dissolved (in 0.1N KOH), continuous, non-pedunculate spermatophores (Fig. 7) are revealed. Here is final evidence that the arches (*a*) never completely close forming distinct ampulla and that the arches are in reality never raised above the broad basal foot (*b*).

DISCUSSION

Mouchet (1931) assigns nine regions of activity to the vas deferens of the typical pedunculate spermatophore producing hermit crab, *Diogenes pugilator* Roux (Matthews, 1953: 264). The spermatophoric differences observed in *A. strigatus* and *A. maximus* are attributed to vasa deferentia which lack one or more of these regions. We are especially concerned in this discussion with region 4, in

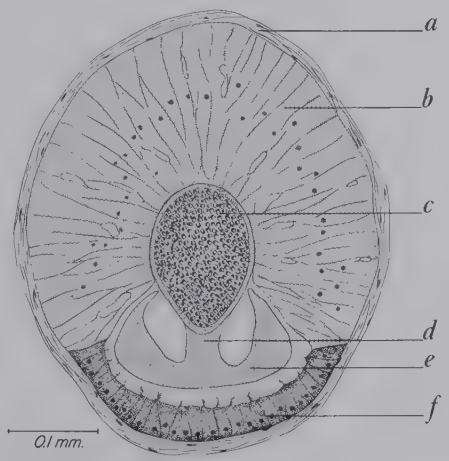

FIG. 5. Cross section of the proximal vas deferens of *Aniculus maximus* (through region 5 of Fig. 2) showing: *a*, muscle layer; *b*, elongate epithelial cells; *c*, sectioned portion of arch; *d*, stalk precursor; *e*, foot; *f*, foot-forming epithelial cells.

which each ampulla acquires a short thick stalk, and with region 6, in which the stalks are stretched.

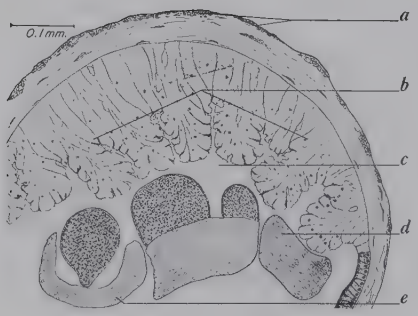

FIG. 6. Portion of cross section through enlarged distal vas deferens of *Aniculus maximus* showing: *a*, circular and longitudinal muscles; *b*, typhlosole-like region of epithelial cells; *c*, mucus-like matrix; *d*, longitudinal section through portion of spermatophore; *e*, cross section through portion of spermatophore.

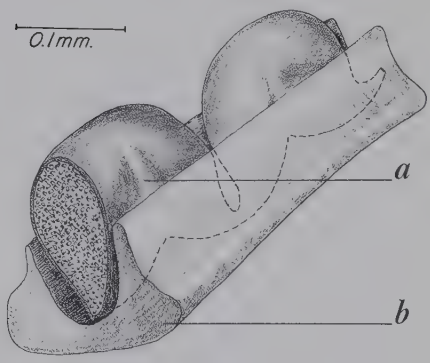

FIG. 7. A composite drawing of vitally stained extruded spermatophores of *Aniculus strigatus* or *Aniculus maximus* (with matrix dissolved away) showing: *a*, unclosed arch not elevated above foot; *b*, foot.

In my observation of the stained cross sections of *A. maximus* I am unable to determine with certainty whether region 4 is present or not. True, both cross and longitudinal sections reveal a "stalk precursor" which fills the spaces of the closing arches but this material, with the stains employed, could not, either in texture or staining affinity, be differentiated from that of foot. It is not the intent of this paper to base pedunculation on whether or not the "stalk precursor" is a separate and distinct secretion from that which forms the foot, but rather to point out that, despite its origin, region 6, where this secretion should be stretched, is lacking. The lack of this region has a pronounced effect on the ultimate elaboration of the spermatophores, for without it the arches are never truly "elevated above" the floor of the foot. That they may appear so in isolated cross sections of the vas deferens (Figs. 3, 4, 5) points to the need to consider both cross and longitudinal sections before statements concerning raised isolated ampullae can be made. Taken alone, Figure 3 and especially Figures 4 and 5 convey the erroneous impression that, indeed, the closed arches form isolated ampullae and that these are elevated on short stalks above the broad basal foot. In reality this is not true, as is seen when Figures 3, 4, and 5 are studied in relation to their position in the longitudinal section of the vas deferens (Fig. 2, regions 3, 4, 5).

This condition in *A. strigatus* and *A. maximus* is not new. Mouchet (1931) points out that the hermit crabs *Eupagurus bernhardus*, *E. prideauxi*, *E. cuanensis*, *Anapagurus hyndmanni*, and *Clibanarius misanthropus* likewise lack regions 4 and 6 in which the stalk is secreted and stretched. Although I have not investigated the spermatophoric development of these hermit crabs, it appears rather unlikely that distinct ampullae of sperm are elevated above the foot. If not, the spermatophores of these hermit crabs should be included with those of *A. strigatus* and *A. maximus* as further evidence of non-pedunculate spermatophore formation in the Paguridae.

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CHAPTER 7

ECOLOGICAL FACTORS INVOLVED IN THE UPTAKE, ACCUMULATION, AND LOSS OF RADIONUCLIDES BY AQUATIC ORGANISMS [1]

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Introduction

THIS paper is concerned with the uptake, accumulation, and loss by living organisms, of radioactive materials that may be added to or induced in an aquatic environment. These aquatic organisms may live in either fresh, salt, or brackish water and include vascular plants, algae, protozoans, plankton, all the other invertebrate forms such as aquatic insects, bottom-living crustaceans and molluscs, and representatives of each of the five classes of vertebrate animals.

The accumulation and loss of any radioisotope will depend not only upon its own physical half-life but also upon the biological factors that contribute to its incorporation in, retention by, and disappearance from the organism involved. In general, all isotopes of any one chemical element are similar in chemical behavior, and thus it can be assumed, when tracing the paths of most chemical elements through biological systems, that a radioactive atom will behave in the same way as a non-radioactive atom of the same species. However, relatively little is known about the actual mechanisms of uptake, accumulation, and loss by marine and fresh-water organisms of the elements whose isotopes constitute fission products and other radiomaterials.

For the purposes of this discussion, the following terms will be defined:

Uptake is the amount of material that enters the organism in question and the speed at which the material enters is the rate of uptake.

Loss is the amount of material that leaves the organism, and the speed at which it leaves is the rate of loss.

Accumulation is the amount of material that is present in the organism at a given time, and the rate of accumulation is the amount accumulated per unit time. In practice, the accumulation is the difference between the uptake and the loss.

Metabolic processes include all the chemical changes concerned in the building up and destruction of living protoplasm. During these changes, energy is provided for the vital processes and for the assimilation of new materials.

Specific activity is the ratio between the amount of radioactive isotope present and the total amount of all other isotopes of that same element, both radioactive and stable. Most commonly, it is given as the microcuries of radioisotope per gram of total element.

Although the higher animal forms are dependent upon the primary concentrators, the plants, for their source of energy, these animals may or may not be dependent upon the lower forms for many elements. Some elements may enter the bodies of the higher forms directly from the water, while others must be supplied from the lower trophic levels through the food web. These food webs are not the same for all organisms and may even be different for the same organism at various seasons of the year. In some instances certain elements, although present in the environment, are not in the proper physical and/or chemical state to be utilized by the organisms and thus are not available for metabolism.

Radionuclides may become associated with an organism either through adsorption to surface areas, through engulfment, or through metabolic

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processes; in some instances assimilation may take place following the engulfment of living or inert particulate matter. A radionuclide may also be incorporated into an organism by simple exchange of the radioactive isotope for the stable isotope of the same species. It is therefore important to know the physical and chemical state necessary for metabolism, the mode of entry, and the ability of all organisms at each of the different trophic levels to concentrate the various radionuclides.

Physical and Chemical Factors Concerned with the Uptake of Radionuclides by Living Organisms

a. *Acute versus chronic exposure*

Chronic exposure of an aquatic organism, even to low concentrations of radiomaterials, usually has a markedly different effect on the organism than an acute exposure; the principal difference lies in the amount of radiomaterial accumulated in the tissues. Because many aquatic organisms have the ability to concentrate radiomaterials from their environments by factors up to several hundred thousand, much radiomaterial may be accumulated during a chronic exposure for a relatively long period of time. A state of equilibrium is ultimately reached at which there is a constant uptake and a constant loss with a resultant constant maximum level of accumulation. Conversely, in an acute exposure, such as a single feeding or a single injection of radiomaterials, only a certain relatively small fraction of the radiomaterial is accumulated in the body and the remainder is lost. In such an instance, the maximum level to which an organism is capable of accumulating the radiomaterial in question is seldom reached and certainly not maintained.

Krumholz and Rust (1954) reported an accumulation of one microcurie of strontium 90 per gram of bone in the entire skeleton of a muskrat (*Ondatra zibethica*) which had been utilizing foods of its own choice in the area contiguous to the Oak Ridge National Laboratory. Certainly this instance can be presumed to represent a chronic exposure inasmuch as the animal was at least two years old and had probably lived in the area during her entire lifetime. Aquatic organisms in the Columbia River below the Hanford Works and those in White Oak Creek, Tennessee, below the Oak Ridge National Laboratory, have all suffered chronic exposures to radiomaterials and have accumulated considerable amounts of those materials in their tissues. Hiatt, Boroughs, Townsley, and Kau (1955) found that the daily feeding of strontium 89 to the fish *Tilapia* for short periods of time (four days) did not increase the level of strontium retention after an apparent steady-state condition had been reached. However, there are no published reports of the results of long-term, controlled experiments of chronic exposures of aquatic organisms to radiomaterials.

The literature contains many reports concerned with acute exposures of aquatic organisms to radiomaterials. Martin and Goldberg (unpublished data), who gave single feedings of strontium 90 to Pacific mackerel (*Pneumatophorus japonicus diego*), found that less than five per cent of the amount fed was retained in the body after 48 hours. Much of the five per cent that was incorporated in the skeleton remained there for the duration of the experiment (235 days). Boroughs et al. (1956) reported that between only one and two per cent of the strontium 89 fed to ten yellowfin tuna (*Neothunnus macropterus*) remained in the body after 24 hours. The small amount retained in the body was largely incorporated into the skeletal structures. However, other fish (*Tilapia*) which had been fed similarly prepared strontium 89 capsules retained about 20 per cent of the ingested material after 24 hours. After four days, the amount retained finally levelled off at values that ranged from 1.5 to 19.5 per cent of the amount ingested; the average amount retained was about 7.5 per cent. Here, again, the retained materials were incorporated mainly in the skeletal structures and integument.

b. *Chemical and physical states of the elements in the environment.*

The chemical composition of the marine environment cannot be rigorously defined. The concentrations of elements depend upon the type and location of the water mass. Although more than 90 per cent of marine waters occur at depths greater than 1000 meters, the majority of chemical analyses have been made for shallower waters. Because of the biological activity of the oceans and the movements and origins of water masses, the abundance of certain elements appears to vary by factors greater than two orders of magnitude. However, as a

first approximation, the chemical constituents may be considered to be much the same in all places. Fairly good approximations of the concentrations of elements in sea water are listed in Table 1 as the numbers of atoms per million atoms of chlorine. The reported values of concentrations of elements on which Table 1 is based frequently fail to distinguish between the solid and dissolved phases.

Whereas the oceans may be considered very roughly as a homogeneous mass, most bodies of fresh water must be examined on an individual basis because of the tremendous range in their physical and chemical characteristics. Many of the elements that occur normally in the oceans are in concentrations too small to be detected by present methods or are present in only trace amounts in fresh water. The pH of fresh waters ranges from perhaps as low as 2.2 to a high of about 10.5 although the pH of most lakes and streams falls somewhere between 6.5 and 8.5. The total dissolved solids in fresh waters ranges

TABLE 1 Chemical Abundances in the Marine Hydrosphere

	mg/l	atoms/10^6 atoms Cl		mg/l	atoms/10^6 atoms Cl
H	108,000	202,000,000	Ag	0.0003	0.005
He	0.000005	.002	Cd	0.000055	0.0009
Li	0.2	50	In	< 0.02	< 0.3
Be			Sn	0.003	0.05
B	4.8	830	Sb	< 0.0005	< 0.008
C	28	4,300	Te		
N	0.5	70	I	0.05	0.7
O	857,000	100,000,000	Xe	0.0001	0.001
F	1.3	130	Cs	0.0005	0.005
Ne	0.0003	0.03	Ba	0.0062	0.008
Na	10,500	850,000	La	0.0003	0.004
Mg	1,300	100,000	Ce	0.0004	0.005
Al	0.01	0.7	Pr		
Si	3	200	Nd		
P	0.07	4	Pm		
S	900	52,000	Sm		
Cl	19,000	1,000,000	Eu		
A	0.6	28.5	Gd		
K	380	18,000	Tb		
Ca	400	19,000	Dy		
Sc	0.00004	0.002	Ho		
Ti	0.001	0.04	Er		
V	0.002	0.08	Tm		
Cr	0.00005	0.002	Yb		
Mn	0.002	0.07	Lu		
Fe	0.01	0.3	Hg		
Co	0.0005	0.02	Ta		
Ni	0.0005	0.02	W	0.0001	0.001
Cu	0.003	0.09	Re		
Zn	0.01	0.3	Os		
Ga	0.0005	0.01	Ir		
Ge	< 0.0001	< 0.003	Pt		
As	0.003	0.07	Au	0.000004	0.00004
Se	0.004	0.1	Hg	0.00003	0.0003
Br	65	1,500	Tl	< 0.00001	< 0.00009
Kr	0.0003	0.007	Pb	0.003	0.03
Rb	0.12	2.2	Bi	0.0002	0.002
Sr	8	160	Po		
Y	0.0003	0.006	At		
Zr			Rn	9.0×10^{-15}	8.0×10^{-14}
Nb			Fr		
Mo	0.01	0.2	Ra	3.0×10^{-11}	2.0×10^{-10}
Tc			Ac		
Ru			Th	0.0007	0.006
Rh			Pa	0.003	0.03
Pd			U		

from very low concentration (less than 5 ppm) in the "battery-water" lakes to very high concentrations (more than 400 ppm) in the "alkali" lakes. The fertility of fresh waters ranges from the almost sterile bog lakes to the highly productive lakes in the midwestern prairies.

The physical states and ionic speciation of elements in sea water cannot be as well defined as their absolute concentrations. However, using the known physicochemical constants, and assuming a pH of 8 and a salinity of 35 parts per thousand for sea water, Krauskopf (1956) postulated that the principal valence states of the ions of a number of metals in sea water are as listed in Table 2. From these data it may

TABLE 2 Calculated Valence States for Metallic Ions in Sea Water
(From Krauskopf, 1956)

Element	Ion
Zinc	Zn^{++}, $ZnCl^{+}$
Copper	Cu^{++}, $CuCl^{+}$
Bismuth	BiO^{+}
Cadmium	$CdCl^{+}$, $CdCl_2$
Nickel	Ni^{++}, $NiCl^{+}$
Cobalt	Co^{++}
Mercury	$HgCl_4^{-}$
Silver	$AgCl_2^{-}$
Gold	$AuCl_4^{-}$ (Calculated by Goldberg)
Chromium	CrO_4^{-}
Vanadium	$H_3VO_4^{-}$, $H_3V_2O_7^{-}$
Magnesium	Mg^{++}
Calcium	Ca^{++}
Strontium	Sr^{++}
Barium	Ba^{++}

be concluded that most monovalent or divalent ions, except the noble metals, will occur as cations whereas most metals with valences higher than two, and the noble metals, will occur as anions.

The physical states of a given element under equilibrium conditions depend upon whether or not the solubility product of the least soluble species has been exceeded. Greendale and Ballou (1954) have determined the distribution of elements among the soluble, colloidal, and particulate states by simulating the conditions of an underwater detonation of an atomic bomb. Their data are presented in Table 3.

It is not known whether the elements that occur in colloidal or particulate phases are homogeneous entities or are sorbed in other solid phases. Nevertheless, it appears that elements of Groups, I, II, V, VI, and VII usually occur as ionic forms in sea water, whereas other elements, excluding the rare gases, occur predominantly as solid phases. These generalizations have been confirmed in field tests after underwater detonations where more than 50 per cent of the resultant radioactivity was associated with solid phases retained by a molecular filter of pore size 0.5 micron (Goldberg, unpublished data).

Although the data supplied by Greendale and Ballou (1954) are of value for the physical states of elements following the detonation of an atomic bomb, they are at best only suggestive of the steady-state conditions which might result from the continuous spilling of fission product wastes into the sea on a long-term basis.

TABLE 3 Physical States of Elements in Sea Water

(From Greendale and Ballou, 1954)

Element	Percentage in given physical state		
	Ionic	Colliodal	Particulate
Cesium	70	7	23
Iodine	90	8	2
Strontium	87	3	10
Antimony	73	15	12
Tellurium	45	43	12
Molybdenum	30	10	60
Ruthenium	0	5	95
Cerium	2	4	94
Zirconium	1	3	96
Yttrium	0	4	96
Niobium	0	0	100

Metabolic processes concerned with the uptake, accumulation, and loss of radionuclides

There are many factors concerned with metabolic processes which are to be considered among the biological aspects of the accumulation of radiomaterials. It has been demonstrated that the metabolism of all forms of life is remarkably similar at the cellular level even though the morphological differences among aquatic organisms range from the bacteria through the vertebrate forms, and from the algae through the vascular plants. Nevertheless, differences do exist. These differences are governed by the complex anatomies, life histories, and physiological processes, and the relationships of the organisms with each other and with their environment. All of these differences must be considered in the light of the physical and chemical states of the elements involved.

In different organisms, ionized or particulate fission-product wastes and other radiomaterials may be either adsorbed, engulfed, or accumulated by metabolic processes. For example, Rothstein and his associates (1951) demonstrated that uranium as the uranyl ion was adsorbed by yeast cells. Hamilton and co-workers (see Hevesy, G., 1948, p. 441) showed that particulate radiomaterials such as various uncomplexed rare earths at physiological pH's were adsorbed by the gut lining of rats. In these experiments practically no accumulation of these particular radiomaterials by the animal was observed. On the other hand, Goldberg (1952) demonstrated with radioactive iron that a marine diatom assimilated particles of hydrated iron oxide, but that these organisms were unable to take up ionic iron in a complexed form.

The first biological experiments in which radioactive atoms were used were performed by Hevesy in 1923. In those classical experiments it was demonstrated that plants could take up lead from solution and translocate it throughout the vascular system.

The accumulation of radioelements is also dependent upon many chemical characteristics of the water in question. Among the parameters affecting accumulation are the salinity, percentage composition of the dissolved solids, pH, the oxygen-carbon dioxide ratio, and the presence of complexing agents.

a. *Chemical composition of marine organisms*

A modern systematic study of the inorganic constituents of marine organisms is yet to be made. The best summary of existing knowledge may be found in Vinogradov (1953).

However, certain generalizations can be drawn from the recent literature on the concentration of metals by marine organisms. Goldberg (in Treatise of Marine Ecology, volume II, edited by J. Hedgpeth, in press) has pointed out that the marine biosphere tends to concentrate such heavy metals as copper, nickel, zinc, etc., over the marine hydrosphere by factors of 100 to 100,000 on a weight-for-weight basis (Table 4). These metals are strongly bound in the organisms and cannot be easily removed by elution. Further, the elements most strongly concentrated in the biosphere are those that form the most stable complexes with organic chelating agents. As an example, copper is concentrated over sea water in the soft parts of most marine organisms by factors of 10^2 to 10^4 whereas calcium shows concentration factors of less than 1 to 50. Copper forms very strong complexes with many organic compounds whereas calcium does not. Although the exact role of most metals in the physiology of organisms is not known, nevertheless, one might *a priori* expect that some heavy metals introduced into the ocean from nuclear reactions would concentrate in the biosphere.

b. *Concentration in the environment*

The concentration of a given radiomaterial by an organism is sometimes proportional to the concentration of that material in the environment. This generalization applies both to aquatic and to terrestrial organisms. The uptake of cesium 137 by the oyster (*Crassostrea virginica*) has been shown to be dependent upon the external concentration of cesium in the sea water (Chipman, et al., 1954). Prosser, et al. (1945), noted that with the addition of strontium to the environment there was an increase in the uptake of that element by goldfish (*Carassius auratus*). Also, it has been demonstrated that as the carrier concentration in the nutrient environment is increased, the concentration factor for a particular fission product in terrestrial plants tends to increase (Rediske, et al., 1955).

c. *Effect of the presence of one element on the uptake of another element*

The uptake of one radioelement by an organism may be altered by the relative abundance of another element in the environment. In instances in which more than one element is involved, one of three phenomena may be observed:

First, elements of similar chemical properties may substitute for one another. For example, it has been shown by Prosser, et al. (1945), that when the amount of calcium in the water was low, there was an increase in the uptake of strontium 89 by goldfish. Conversely, as the amount of calcium was increased, the uptake of strontium decreased. Rice (1956) observed that cells of *Carteria* grown in artificial sea water took up strontium in proportion to the strontium/calcium ratio in the medium. Bevelander and Benzer (1948) have shown that a modification of the constituents of sea water resulted in a change in the constituents of the shells deposited by mollusks.

Second, some elements may have an inhibitory effect on others. A classical example of this

phenomenon is that in which calcium inhibits the stimulatory action of potassium on heart muscle.

Third, there may be a synergistic effect of one element on another. Ketchum (1939) has shown that the uptake of phosphorus by marine diatoms was enhanced with increased concentrations of nitrogen.

d. *Specificity of organisms and tissues for given elements*

The specific activity of a radionuclide in any organism is dependent upon the ability of the organism or any of its parts to concentrate that nuclide. If the stable counterpart of the radionuclide does not normally enter into the physiological processes of an organism, neither will the radioactive material.

It is well known that certain tissues have a predilection for concentrating specific elements. For instance, iodine is concentrated in the thyroid tissue of animals and hence radio-iodine will also be concentrated there. Strontium, like calcium, is a bone seeker and the radioisotopes of both of those elements will be concentrated in the bony skeletons of animals. Similarly, both strontium and calcium are concentrated in certain parts of vascular plants and so are the radioisotopes. Phosphorus is one of the principal constituents of bone and radiophosphorus is also concentrated in that tissue. The compound adenosine triphosphate is commonly present in the flight muscles of some birds and it has been shown that radiophosphorus is incorporated into the flight muscles of migratory waterfowl (Krumholz, 1954).

Although many different kinds of aquatic organisms have the ability to concentrate phosphorus in their tissues, there are few that show such a specificity for that element as the various plankters. The uptake of phosphorus 32 by plankton algae in a lake has been demonstrated by Coffin and his associates (1949) and others, and Whittaker (1953) showed that phytoplankters from the Columbia River concentrated radiophosphorus by factors as great as 300,000. Krumholz (1954, 1956) found that attached fresh-water algae (*Spirogyra*) concentrated radiophosphorus by a factor of 850,000, and that many fresh-water zooplankters concentrated that radionuclide by factors of more than 100,000. Approximate concentration factors for marine organisms are given in Table 4.

TABLE 4 Approximate Concentration Factors of Different Elements in Members of the Marine Biosphere. The Concentration Factors are Based on a Live Weight Basis.

Element	Form in Seawater	Concentration in seawater (micrograms/l.)	Algae (Non-calcareous)	Concentration Factors: Invertebrates Soft	Invertebrates Skeletal	Vertebrates Soft	Vertebrates Skeletal
Na	Ionic	10^7	1	0.5	0	0.07	1
K	Ionic	380,000	25	10	0	5	20
Cs	Ionic	0.5	1	10	—	10	—
Ca	Ionic	400,000	10	10	1,000	1	200
Sr	Ionic	7,000	20	10	1,000	1	200
Zn	Ionic	10	100	5,000	1,000	1,000	30,000
Cu	Ionic	3	100	5,000	5,000	1,000	1,000
Fe	Particulate	10	20,000	10,000	100,000	1,000	5,000
Ni[1]	Ionic	2	500	200	200	100	—
Mo	Ionic-Particulate	10	10	100	—	20	—
V	?	1	1,000	100	—	20	—
Ti	?	1	1,000	1,000	—	40	—
Cr	?	0.05	300	—	—	—	—
P	Ionic	70	10,000	10,000	10,000	40,000	2,000,000
S	Ionic	900,000	10	5	1	2	—
I	Ionic	50	10,000	100	50	10	—

[1] Values from Laevastu and Thompson (1956).

e. *Osmotic and ionic regulation*

Osmotic and ionic regulation are known to occur in a variety of ways. The usual pathways of excretion are through the urine, feces, skin, respiration, and particle ejection, and the method of excretion depends upon the particular organism and element involved. Ionic regulation may also occur by way of the chloride secreting cells in the gills of those fishes that migrate from salt to brackish water (Keys,

1931). Unfortunately, no experiments on such ionic regulation have been performed with radionuclides.

f. *Reproductive processes*

The reproductive processes of plants and animals range from simple fission among the unicellular organisms to the very complex relationships among the gametogenic forms. During reproduction there is a transfer of materials from the parent to the offspring.

In simple fission, the parent cell splits in two and each offspring receives approximately half of the parent material and thus only half of any radiomaterial that may have been present. Under conditions of chronic exposure, the offspring of organisms that reproduce by fission will incorporate usable radiomaterials into their bodies and a state of equilibrium eventually will be reached.

Among the egg-laying forms, most of the material received by the offspring is derived from the contents of the egg. In this form of reproduction, once the egg is laid there will be no further loss of radiomaterials from the mother or gain to the offspring. This applies even when the environment is contaminated and there is chronic exposure of the parents, because the protective coverings of the egg prevent the entrance of radiomaterials.

Among the forms that bear their young alive, however, there is usually some continuous transport of materials between the mother and the embryo. In such an instance it is probable that the embryo will accumulate radiomaterials with a resultant loss to the mother. If chronic exposure of a mother carrying an embryo continues during pregnancy, a state of equilibrium may eventually be reached between the mother and the environment and between the mother and the embryo.

During embryological development of all kinds there is a "biological dilution" of radiomaterials through cell division and growth. This statement applies primarily if there has been an acute exposure to radiomaterials or if the exposure has stopped with the commencement of the embryological development.

g. *Molting*

In instances where the embryos pass through a series of metamorphic stages, there is a loss of radiomaterials from stage to stage as, for example, the loss from instar to instar in insects through molting. Furthermore, it has been demonstrated by Chipman and coworkers (personal communication) that there is an increased accumulation of elemental constituents in crustaceans prior to molting, and a loss of such materials when the carapace is lost.

h. *Age and growth*

It has been established (Olson and Foster, 1952) that younger, more rapidly growing fishes accumulate relatively greater amounts of radiomaterials than do older, more slowly growing individuals. This phenomenon is probably a reflection of the more rapid metabolism that accompanies the growth of the younger fishes. It is not known whether the accumulation of radiomaterials by other aquatic vertebrates and invertebrates is a function of age and growth.

i. *Effect of temperature on cold-blooded and warm-blooded animals*

In general, the body temperatures of warm-blooded animals are more or less constant whereas the body temperatures of cold-blooded animals largely depend upon the temperature of the environment. Similarly, the rate of metabolism in warm-blooded animals is generally independent of temperature changes in the environment while that in the cold-blooded animals is largely dependent upon external temperatures. Changes in temperature affect the rates of chemical reactions and hence chemical processes that involve the accumulation of elements in the body tissues are temperature dependent.

Generally speaking, all cold-blooded aquatic organisms exhibit seasonal changes in the uptake and accumulation of radiomaterials from the environment. Davis, et al. (1953), and Krumholz (1954, 1956) have shown that there is a direct correlation between an increase in temperature and an increase in the accumulation of radiomaterials in fishes of the Columbia River, Washington, and of White Oak Lake, Tennessee, respectively. This increase in accumulation is apparently a reflection of the increase in the speed of the metabolic processes with rising water temperatures. However, Krumholz (1956) suggested that the fishes in White Oak Lake entered a period of dormancy following August 1 and lost about two-thirds of their accumulated radioactivity during the subsequent two months even though the water temperatures were much the same as they were during the earlier part of the summer.

In studies of the uptake of strontium 89 by

oysters and other shellfish at the Radiation Laboratory of the Fish and Wildlife Service (Chipman, unpublished data) it was found that the rate of uptake was slowed down and the retention time was extended when the animals were kept in sea water at low winter temperatures. Conversely, the rate of uptake was speeded up and the retention time was shortened when the animals were kept at summer temperatures. In other experiments at the same laboratory, it was found that larvae of the winter flounder (*Pseudopleuronectes americanus*) took up strontium 89 much more rapidly at higher water temperatures than at lower.

So far as is known, there is no demonstrable seasonal pattern of accumulation of radiomaterials among the warm-blooded aquatic vertebrates. It is generally believed that inasmuch as the body temperatures of those animals remain more or less constant throughout the year there will be no marked seasonal changes in the uptake of radiomaterials based on changes in rates of metabolism.

j. *Effect of light*

Light affects the uptake and accumulation of radioelements by plants. For example, it has been clearly shown by Scott (1954) that the uptake of radiocesium by the algae *Fucus* and *Rhodymenia* was greatly enhanced in the presence of light.

k. *Radiation effects*

Many aquatic organisms have the ability to concentrate radiomaterials in amounts deleterious to their well-being. These deleterious effects range from those in which only the individual is concerned to those in which the population as a whole may be affected. Elsewhere in this series of reports there is a paper on the effects of radiation on aquatic organisms.

Aspects of the accumulation of radionuclides through the ecosystem

For purposes of this paper, the aquatic biosphere can be divided into three trophic levels based on energy sources:

1. Primary producers, such as the photosynthetic plants.
2. Primary consumers, the herbivores, such as water fleas (cladocerans).
3. Secondary consumers, the carnivores, such as the largemouth bass or the tunas.

The community biomass (the total weight of all organisms in the community) is unequally divided between the three trophic levels. Usually there is a progressive decrease in both the biomass and the number of organisms from the first trophic level through the third, and a progressive increase in the size of the organisms. However, most community populations are constantly changing and are affected by seasonal, diurnal, and other cycles of abundance. These changes frequently have a profound effect on the environment and any changes in the environment in turn affect the stability of the community.

Generally speaking, the smaller organisms have a higher reproductive potential, a shorter life span, and a shorter time between generations; the length of the life span and the time between generations usually give a fair indication of the length of the embryological period. Furthermore, the smaller animals usually serve as food for the larger ones.

The discussion will consider the following aspects of the accumulation of radiomaterials in the three trophic levels: (1) the distribution of elements among the three levels, (2) the concentration factors in different organisms within the same level, and (3) the transport of radiomaterials from one trophic level to another.

Problems of the distribution of radionuclides among the trophic levels and the degree of concentration of radionuclides by different organisms can be approached most readily through separate consideration of the effects from an acute exposure and those from a chronic exposure.

A steady-state condition will be approximated when the amounts of radiomaterials introduced into the environment is equal to the amount that disappears through physical decay. Any organisms living in such an environment will suffer chronic exposure to the radioactivity, the level depending, of course, on their ability to concentrate the radiomaterials introduced and on the steady-state concentration of these materials in the surrounding medium. An approximation of the concentration factors for some organisms is given in Table 4.

Davis and co-workers (1952) showed that there was a progressive decrease in the amount of radioactivity found in the aquatic organisms of the Columbia River downstream from the Hanford Works. There, the principal radionu-

clide was phosphorus 32, which has a physical half-life of about 14 days. It is apparent that when following the steady-state transport of radiomaterials through the ecosystem the following parameters must be considered: (1) the physical half-life of the radionuclide, (2) the distance of the organism from the source of radioactive contamination, and (3) the dilution of the radiomaterials between the point of introduction and the area in which the organism lives.

The results from acute exposure cannot be as definitely approximated as for chronic exposure. In such instances, the time element is very important, and the following must be known: (1) the rate of dilution of the radioactive water mass with non-radioactive water; (2) the rate of transfer of radiomaterials from one trophic level to another with the concurrent dilutions and losses or gains in concentration by the organisms; and (3) the life span of the organisms involved.

In general, the radiomaterials taken up by organisms of the first trophic level will be primarily in the ionized state although a certain amount of particulate radiomaterials will be adsorbed to the body surfaces. When uptake occurs, the rate of uptake will probably be more rapid than the rate of uptake in the other trophic levels.

Particulate radiomaterials tend to be concentrated in the second trophic level. Findings from the Wigwam and Castle tests (Goldberg, unpublished data) showed that the principal organisms which concentrated particulate radiomaterials were the mucous, ciliary, and pseudopodial feeders among the zooplankters. These organisms contained much more radioactivity per unit weight than either the algae or the setal or rapacious feeders.

In addition to the differences in concentration of radiomaterials from one trophic level to another, there are marked differences among species in the same level. For instance, it has been shown by Chipman, et al. (1953), that some phytoplankters will concentrate radiostrontium by a factor of about 20 times whereas others will concentrate the radioelement by factors as much as 1500 times. Comparable data have been recorded by Krumholz (1954) for the accumulation of radiophosphorus by the phytoplankters of White Oak Lake.

Differences also exist between individuals of the same species. Very large differences in the amounts of radiomaterials accumulated by individual fishes in White Oak Lake were described by Krumholz (1956). For instance, he reported that the amounts of radiostrontium in the bones of three bluegills (*Lepomis macrochirus*) differed by more than five-fold. These three fish were taken from the same place in the lake on the same day, August 27, 1952. Comparable differences were found in the amounts of accumulated radiomaterials in most other tissues.

The transfer of radiomaterials from one trophic level to another is not only dependent upon the concentration of the radiomaterial in the organism but also is governed by the rate of growth of the organism and the rate of increase in the size of the population. These factors of transfer are of particular importance in the event of an acute exposure because the dilution brought about through cell division and growth may well minimize any radiation effect. In any event, there is always a loss in the total amount of radiomaterials in the transfer from one trophic level to another (though not necessarily a decrease in the concentration in individual organisms). Such a loss may be relatively small or it may be very great depending upon the organism and the particular food web involved.

Not all radiomaterials that enter the first trophic level are passed on to higher levels. At each trophic level there are certain species that, for one reason or another, are not widely used as food by the organisms of higher levels. Also, some of the plants of the first trophic level may die before they are eaten and thus will be returned to the environment as organic matter. In this case the primary producers may be of little or no importance as a source of radiomaterials to the organisms of the second and third trophic levels.

If relatively large quantities of radiomaterials are accumulated in certain hard parts of an organism, such as the shell of an oyster or the bones of a fish, they will, in all probability, remain in those parts during the greater part of the life of the animal concerned, and will not be available to other animals in the biosphere until the animal dies.

Chipman and co-workers (1953) showed that oysters fed on *Chlorella* assimilated only very little of the radiophosphorus from these

algae. On the other hand, oysters fed upon other phytoplankters that contained no more radiophosphorus than the *Chlorella* accumulated relatively large amounts of radiophosphorus and incorporated that element into their tissues as organic phosphorus compounds. It appears that the particular food web used by any organism is of primary importance in the transfer of radiomaterials from one trophic level to another.

Problems for further research

One of the fundamental questions to be answered concerns the mechanism of incorporation of the heavier elements, such as the fission products, in aquatic organisms. To date, no metal heavier than molybdenum has been shown to be necessary for metabolic processes. Specifically, we need to know:

1. How are the radioactive elements passed through membranes and where and why do they concentrate in the organisms?
2. What are their biological half-lives of the different radioactive elements in different organisms?
3. What are the average and extreme concentration levels of these elements in various organisms and in the biosphere?

The revolution in biological thought brought about by the use of labelled atoms is manifest in all branches of biological research today. Radioisotopes have permitted the study of rate processes that could not have been investigated in any other way. Such processes include the pumping rates of water and other biological fluids, and the transfer of molecules or portions of molecules from tissue to tissue, or, on the ecological level, from organism to organism.

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LABORATORY EXPERIMENTS ON THE UPTAKE, ACCUMULATION, AND LOSS OF RADIONUCLIDES BY MARINE ORGANISMS

Chapter 8

LABORATORY EXPERIMENTS ON THE UPTAKE, ACCUMULATION, AND LOSS OF RADIONUCLIDES BY MARINE ORGANISMS [1]

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What happens to radioactive materials that are introduced into the oceans may be studied by a marine biologist from at least two points of view. As a physiologist, he will be interested in the uptake, accumulation, and loss of radioelements as a function of the element, and its concentration; in the physical factors of temperature, light, and salinity; and in differences between species of organisms, as well as their age and sex, to mention some of the most important parameters. As an ecologist, he will be interested in these same parameters under a steady-state condition. The physiologist would profit most by exposure of the organism to a single dose of radioactive material, while the ecologist must concern himself with the results of chronic exposure.

Both types of biologists may be interested in tracing the history of an element through the food webs of the various trophic levels. Unfortunately, the experimental data involving the metabolism of radionuclides by marine organisms is extremely meager. In this section some experiments will be described on the uptake, accumulation, and loss of radionuclides by various marine organisms in the three trophic levels. It must be emphasized that the results of these few experiments must be extrapolated with extreme caution in predicting what may happen to radioactive materials introduced into the oceans from nuclear reactor plants, bomb detonations, or from any other sources.

In discussing the uptake of radionuclides by marine organisms, it is sometimes difficult to state exactly what constitutes a single or a chronic exposure. For a unicellular alga, a few hours may represent chronic exposure, while a few weeks may be insufficient for a fish to reach a steady-state condition. No long-term repetitive feeding experiments have been done, so for the purpose of this report, we will discuss the metabolism of the various radionuclides solely on the basis of the trophic level concerned.

The term uptake implies passage through a membrane. Radioactive material may be present in the gut of an organism, but until it enters the organism through a membrane, it can play no role in the metabolism of that organism except by producing radiation effects or by interfering with a chemical reaction occurring within the gut. In some of the experiments to be described, particularly those involving phytoplankton, it was not established whether or not the radioisotope was actually incorporated into the organism, or merely adsorbed to the surface. For simplicity, we will therefore discuss uptake in the sense that the radioisotope is associated with the organ or organism in question.

Isotopes of a given element usually have similar chemical behavior, so that in tracing the path of most elements in biological systems, it can be assumed that a radioactive atom will behave in the same way as a non-radioactive atom of the same species. The only parameters to be considered in the discussion to follow will be the species and age of the organism, the element, the concentration of the element, the temperature, and the duration of exposure or treatment. No work using radioisotopes has been

[1] Work performed at the Fishery Radiobiological Laboratory of the U. S. Fish and Wildlife Service and the Hawaii Marine Laboratory (Drs. H. Boroughs, S. J. Townsley, and R. W. Hiatt).

Contribution No. 95, Hawaii Marine Laboratory.

done on the mineral metabolism of marine organisms relative to sex. The data that will be presented were collected either at the Fishery Radiobiological Laboratory of the United States Fish and Wildlife Service (R.L.F.W.S.) or the Hawaii Marine Laboratory, University of Hawaii (HML).

First trophic level

Experiments performed at the R.L.F.W.S. very clearly show that different species of planktonic algae have remarkably different abilities to concentrate a particular element from the sea water medium. Algae were grown in the presence of radiostrontium obtained from Oak

TABLE 1 The Differential Uptake of Radioactive Strontium and Yttrium By Algae

Species	Percentage activity from strontium	Percentage activity from yttrium
Carteria sp.	100.0	0.0
Thoracomonas sp.	50.4	49.6
Amphora sp.	10.0	90.0
Navicula sp.	8.5	91.5
Chromolina sp.	8.2	91.8
Chlamydomonas sp.	6.5	93.5
Nitzschia closterium	6.0	94.0
Nannochloris atomus	5.7	94.3
Chlorella sp.	5.3	94.7
Porphyridium curentum	4.4	95.6
Gymnodinium splendins	4.1	95.9
Gyrodinium sp.	2.3	97.7

Ridge. The material used contained both Sr^{89} and Sr^{90}; the latter decays to form Y^{90}. By counting the algal samples immediately after they were removed from the culture medium, and again after several weeks, in order to allow the secular equilibrium of the Sr^{90}-Y^{90} pair to be reached, it was possible to determine what percentage of the original radioactivity was due to strontium. Table 1 shows that *Carteria* sp. accumulated strontium 89 and 90 from the isotopic mixture, and that *Gyrodinium* sp. removed almost no strontium 89 or 90, but instead accumulated yttrium 90. It was found that *Nitzschia closterium* under an apparent steady state condition concentrated strontium 17 times over its concentration in sea water (weight of algae/weight of water). The concentration factor for strontium *Carteria* sp. was found to vary with condition of culture but was much greater than for *Nitzschia closterium.*

Experiments using cesium^{137} show that while different species concentrate cesium to different degrees (Table 2) none of the nine species

TABLE 2 Concentration of Cesium By Marine Algae

Algae	Concentration factor [1]
Bacillariaceae	
Nitzschia closterium	1.2
Amphora sp.	1.5
Nitzschia sp.	1.7
Chlorophyceae	
Chlamydomonas sp.	1.3
Carteria sp.	1.3
Chlorella sp.	2.4
Pyramimonas sp.	2.6
Nannochloris atomus	3.1
Rhodophyceae	
Porphyridium curentum	1.3

[1] The concentration factor is reported as the ratio of Cs^{137} in the algae (wet weight) to that in an equivalent weight of sea water at an apparent steady-state condition.

tested from three families showed any marked concentration of this element from sea water.

The effect of the concentration of an element on its uptake by *Nitzschia* cells is shown in Figure 1. *Nitzschia* cells were grown in sea water to which had been added labelled zinc at three different concentrations. From the graph

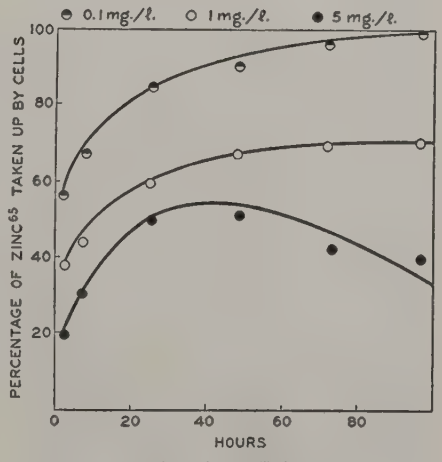

Figure 1. Uptake of $Zinc^{65}$ by *Nitzschia* Cells from Culture Medium Containing Different Concentrations of Zinc.

- 0.1 mg./l
- 1 mg./l
- 5 mg./l

it is evident that at low concentrations all the zinc was removed after about four days. The lowest concentration used was still ten times higher than the average zinc concentration of sea water.

The rate of uptake of zinc^{65} by *Nitzschia* cells is shown in Figure 2. At the normal con-

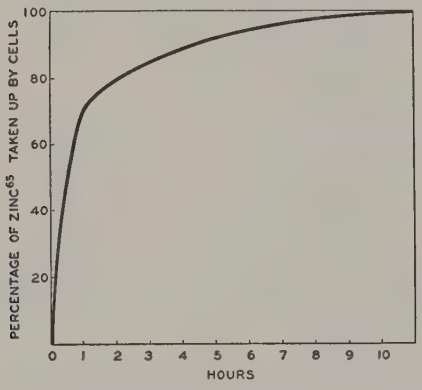

FIGURE 2. Uptake of Zinc^{65} by *Nitzschia* Cells from Culture Medium Containing 10 Micrograms of Zinc/Liter.

centration of zinc in sea water, a dividing culture of *Nitzschia* depleted the zinc^{65} in a closed system in less than one day. Apparently phytoplankton cells concentrate zinc relative to sea water and any radioactive zinc present in the water will be quickly taken up in large amounts.

The radioisotopes so far discussed are very likely always ionic in sea water. Ruthenium solution, however, forms colloids and particles when put into sea water. Ruthenium^{106} obtained as an acid solution from Oak Ridge was added to a sea water culture of *Nitzschia* cells. Figure 3 shows that the cells continued to take up the ruthenium for the 12 days of the experiment. The amount of ruthenium per cell decreased, however, since the cells of the culture were dividing continually. One may conclude from this experiment, that since the ruthenium concentration in sea water is low, dividing planktonic algae would take up large amounts of any radioactive ruthenium present.

Second trophic level

The work reported in this section was also done at the R.L.F.W.S. Larvae of the brine shrimp *Artemia* were put into filtered sea water containing radiostrontium and the daughter

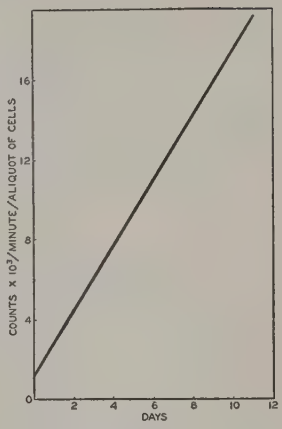

FIGURE 3. Uptake of Ru^{106} by *Nitzschia* Cultures in the Light.

yttrium^{90}. These larvae rapidly took up the SR^{89}-$Sr^{90}Y^{90}$ and reached an apparent steady-state in a few hours. After exposure of the organisms to the isotopes for one day, it was found that the amount of radioactivity/g of *Artemia* was only 70 per cent of that of an equal weight of the sea water. A count of the samples 30 days after their preparation indicated that a considerable amount of Y^{90} was taken up. Other crustaceans used were the shrimp *Penaeus setiferus* and the edible blue crab *Callinectes sapidus*. The molluscan shellfish studied included oysters (*Crassostrea virginica*), clams (*Venus mercenaria*), and scallops (*Pecten irradians*).

All of these organisms accumulated strontium rapidly from sea water. The internal distribution of strontium in oysters is shown in Table 3. This table indicates that the bulk of the radioactivity accumulates in the shell. When

TABLE 3 DISTRIBUTION OF RADIOACTIVITY IN OYSTERS FOLLOWING EXPOSURE TO SEA WATER CONTAINING Sr^{89}

Tissues	Per cent of total weight	Per cent of total activity	Per cent of soft tissues	Per cent of activity of soft tissues
Mantle	2.5	4.1	25.0	27.7
Gills	1.7	3.1	17.5	21.2
Adductor muscle	1.9	2.4	19.2	16.2
Other	3.8	5.1	38.3	34.9
Total soft tissues	9.9	14.7	—	—
Shell	90.1	85.3	—	—

the radioactive shellfish were returned to a normal sea water environment, the radioactivity present in the soft tissues declined within one day to 10 per cent or less of the maximum concentration. This residual amount was held by the tissues for several days.

The uptake of radiostrontium by oysters from food was studied by growing *Carteria* cells in sea water to which Sr^{89} was added. Oysters in Sr^{89} sea water served as the controls; the treated oysters were kept in Sr^{89} sea water to which the labelled *Carteria* cells were added. Fresh sea water and plankton suspensions were prepared each day. The curves in Figure 4 show that an

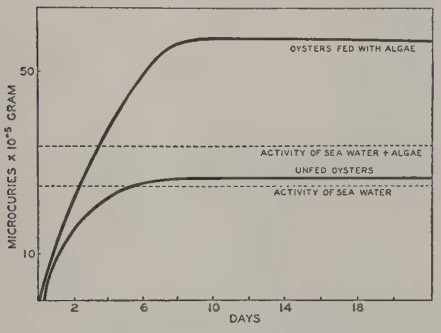

FIGURE 4. The Increased Accumulation of Sr^{89} by Oysters Feeding on Sr^{89}-Fed Algae.

apparent steady-state is reached in eight days. In the unfed oysters the concentration of Sr^{89} in the soft parts is approximately the same as the concentration in the sea water. The oysters which fed on the radioactive algae, however, concentrated the Sr^{89} by a factor slightly greater than two, based on the radioactivity of the suspension per unit of weight. These filter-feeding organisms removed the algal cells from many volumes of water.

The uptake of $cesium^{137}$ by clams, *Venus mercenaria* L., is shown in Figure 5. At the end of 20 days the soft parts of clams had concentrated the cesium by a factor of six over the cesium concentration of sea water. Obviously a steady state had not occurred, so that it is not possible to say what the final concentration factor of clams might be for cesium in solution. Similar experiments using the bay scallop, *Pecten irradians* L., show that the concentration factor of cesium is greater than eight, since the uptake was still increasing at the end of 10 days.

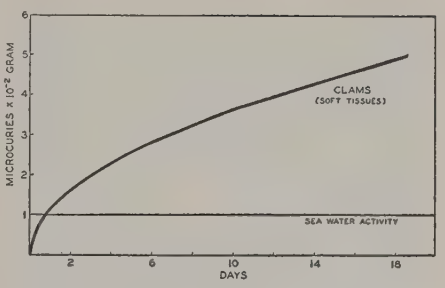

FIGURE 5. The Accumulation of $Cesium^{137}$ by Clams as a Function of Time.

Bay scallops immersed for two hours in sea water containing Zn^{65} very rapidly accumulated this isotope. Table 4 lists the internal distribution of $zinc^{65}$ in the various tissues. The concentration factor for each organ is readily calculated since the activity of the sea water was 10 mμc/g. This means that the figures given in the second column divided by 10 equal the concentration factors. The over-all concentration factor of the soft tissues of the bay scallop was 20 for this short interval. Other observations showed that these scallops contained close to 35,000γ of zinc per gram (wet weight) and thus had a concentration factor for this element of about 3500.

Oysters that were kept in sea water with added Zn^{65} also quickly accumulated the isotope to very high levels. The zinc content of fresh oyster tissue measured almost 170,000γ per gram. This represents a concentration factor of 17,000, since the zinc concentration of the sea water in which the oysters lived was about 10 mcgm/1.

$Ruthenium^{106}$ was one of the separated fission products used to study the uptake of particulate radioisotopes by organisms in the second trophic level. Ruthenium was co-precipitated with calcium carbonate, dried, and ground

TABLE 4 DISTRIBUTION OF Zn^{65} IN THE ORGANS OF THE BAY SCALLOP AFTER A TWO HOUR IMMERSION

Tissue	mμc Zn^{65}/g.	Total mμc
Kidney	1384	824
Liver	243	507
Gills	218	857
Testes and ovaries	138	193
Foot	131	25
Rectum	120	8
Heart	105	13
Adductor muscle	100	375
Mantle	92	321

to a very fine state. Plutei of the sea urchin, *Arbacia punctulata* were put into sea water containing the radioruthenium which was kept in suspension by aerating the culture flask. After 18 hours, the larvae were rinsed and resuspended in fresh sea water. Aliquots of larvae were then removed at intervals and tested for radioactivity (Table 5). A microscopic examination of the larvae at zero time showed that the intestines were filled with the radioactive particulate material, but at 8 hours, very little material was left in the gut. Apparently little ruthenium was actually absorbed through the digestive tract.

TABLE 5 The Decrease of Ru^{106} in Sea Urchin Larvae as a Function of Time in Non-radioactive Water

Hours	Radioactivity in 500 larvae (counts/minute)
1	1413
4	179
8	148

The ingestion of the particulate (co-precipitated) ruthenium by the bay scallop, *Pecten irradians,* also indicated that the radioactivity was mostly associated with the digestive tract. The crystalline style was highly radioactive, although the radioactivity in it decreased during the five days the scallops were kept in running water. The hepatopancreas, on the other hand, showed an increase in radioactivity during this time. No radioactivity was found associated with the internal organs other than those in the digestive tract.

Third trophic level

The uptake, accumulation, and loss of radionuclides has been studied in many fishes by both the R.L.F.W.S. and the H.M.L. These fishes include the skipjack tuna (*Euthynnus yaito*), yellowfin tuna (*Neothunnus macropterus*), dolphin (*Coryphaena hippurus*), papio (*Carangoides ajax*), aholehole (*Kuhlia sandvicensis*), *Tilapia mozambique,* menhaden (*Brevoortia tyrannus*), bluefish (*Pomatomus saltatrix*), little tuna (*Euthynnus allitteratus*), croakers (*Micropogon undulatus*), and king whiting (*Menticirrhus* sp.).

At the H.M.L., strontium^{89} in gelatine capsules was fed to skipjack, dolphin, and yellowfin tuna. These are all fast-swimming pelagic fish. Figure 6 shows that the excretion of strontium is very rapid. In 24 hours, only about two per cent of the dose remains in the fish. Similar experiments with *Tilapia,* a small, sluggish bottom feeder, indicate that the strontium is also mainly excreted, but that the time required to reach a minimum level of about five per cent of the dose requires at least four days. This information is consistent with the idea that the metabolic rates of these fishes are very much different, and the sluggish fish might be expected to retain the strontium for longer periods.

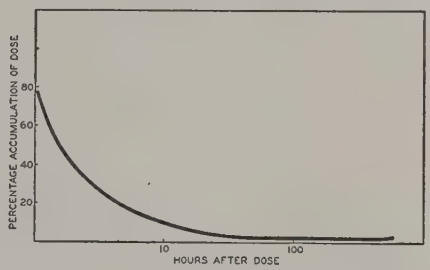

Figure 6. The Percentage Accumulation by Tuna Fish of Sr^{89} Given Orally.

The internal distribution of the total radioactivity recovered is shown in Table 6. By plotting the radioactivity of each organ against time, it is apparent that the soft, visceral tissues rapidly excrete the strontium, but that the bony structures, gills, integument, and muscles retain the strontium for a long period. *Tilapia* show the same behavior. The data are presented in Table 7.

The direct uptake of strontium^{89} in solution by *Tilapia* was also studied at the H.M.L. Figure 7 shows that after about two weeks, the

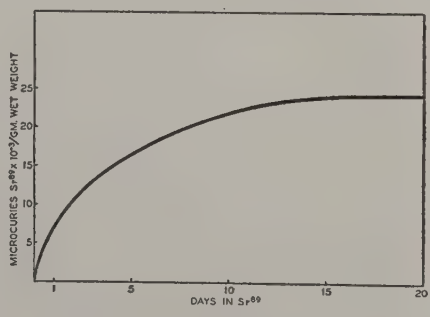

Figure 7. The Uptake of Sr^{89} in Solution by *Tilapia Mozambique.*

TABLE 6 ACCUMULATION OF Sr^{89} IN THE VARIOUS ORGANS AND TISSUES OF TUNA AFTER INGESTION

	Percentage of total activity									
	Dose: 5.55μc	Dose: 480μc	Dose: 240μc	Dose: 51.0μc	Dose: 240μc	Dose: 464μc	Dose: 464μc	Dose: 464μc	Dose: 371μc	Dose: 371μc
Tissue	1 hr	2¼ hr	6 hr	7 hr	11½ hr	24 hr	96 hr	264 hr	480 hr	648 hr
Heart	0.04	0.01	0.03	0.049	0.11	0.05	0.028	0.01	0.014	0.007
Gall bladder	0.05	0.04	0.07	0.10	0.08	0.03	0.0001	0.01	0.004	0.002
Blood	4.21	6.68	15.00	0.85	8.07	2.73	1.14	0.35	0.51	0.12
Gill flesh	12.44	0.18	0.91	8.56	5.06	30.61	25.72	2.42	1.42	2.21
Gill bone		1.34	6.47		26.39			16.80	19.48	22.76
Caecum	37.01	7.67	7.84	2.70	2.64	0.34	0.15	0.05	0.04	0.029
Foregut	0.89	9.32	1.12	0.74	1.03	0.20	0.24	0.04	0.04	0.018
Midgut	2.28	14.16	16.50	1.08	1.48	0.65	0.25	0.05	0.036	0.003
Hindgut	11.78	3.98	21.26	2.26	0.11	0.15	0.024	0.03	0.015	0.016
Gut contents	—	48.32	12.73	0.056	19.65	—	0.10	0.013	—	0.0008
Head, operculum	—	0.41	1.09	24.99	6.28	18.33	24.58	28.18	29.91	24.58
Appendicular skel.	3.60	0.40	1.19	36.21	8.45	23.69	30.32	29.15	30.47	31.43
Liver	3.34	1.48	3.04	0.39	2.46	0.15	0.04	0.03	0.04	0.027
Spleen	0.20	0.32	1.39	0.08	0.60	0.03	0.008	0.03	0.010	0.003
Tail	—	0.42	0.15	—	0.00	—	—	—	—	—
Brain, spinal cord	0.23	0.00	0.01	1.24	0.05	1.66	1.70	1.33	0.030	0.004
Eyes		0.04	0.06		0.60			2.02	1.34	1.34
Integument	5.28	1.69	0.86	10.20	5.89	7.69	11.37	13.73	10.25	10.51
Integument flesh (aliquot)	—	0.01	0.01	—	0.05	—	—	—	—	0.065
Integument scales (aliquot)	—	0.02	0.02	—	0.11	—	—	—	—	0.091
Gonad	2.40	0.09	0.47	0.22	0.08	0.06	0.004	0.03	0.023	0.020
Kidney		0.08	0.16		0.09		0.027	0.07	0.035	0.022
Light muscle	16.23	3.23	8.74	4.19	10.01	12.84	3.94	5.26	5.69	5.79
Dark muscle		0.10	0.86	5.25	0.70	0.72	0.48	0.47	0.63	0.95

TABLE 7 THE INTERNAL DISTRIBUTION AND PERCENTAGE RECOVERY OF A DOSE OF 75 μc OF Sr^{89} BY *Tilapia*

Days after dose	Tissue	Percentage of total recovered
1	Skin	25.27
	Eyes	0.35
	Visceral organs	1.82
	Gills	15.62
	Muscle	5.65
	Skeleton	51.30
	Total	100.01
2	Skin	24.44
	Eyes	0.18
	Visceral organs	1.08
	Gills	8.13
	Muscle	3.10
	Skeleton	63.07
	Total	100.00
4	Skin	24.56
	Eyes	0.25
	Visceral organs	1.01
	Gills	6.42
	Muscle	8.40
	Skeleton	59.35
	Total	99.99

TABLE 7—*Continued*

Days after dose	Tissue	Percentage of total recovered
7	Skin	22.79
	Eyes	0.33
	Visceral organs	1.14
	Gills	10.11
	Muscle	3.01
	Skeleton	62.62
	Total	100.01

uptake apparently levels off at a value which corresponds to a concentration factor of about 0.3. This means that these fish can to some extent exclude the strontium ion in solution. Even the skeleton had not yet come to equilibrium with the radioactivity in the sea water. This may mean that only about 70 per cent of the strontium in the bone is readily exchangeable. The remainder may be firmly bound in a lattice or to an organic matrix which has a slow rate of turnover. It should be emphasized that these fish were mature.

Experiments done at the R.L.F.W.S. with Sr^{89} on post-larval flounders indicate that age

and temperature influence the uptake of elements in solution. One group was kept at 20–22° C in sea water containing Sr^{89}, and another group at 8–12° C. The fish in both groups averaged 0.02 g. each. Figure 8 shows

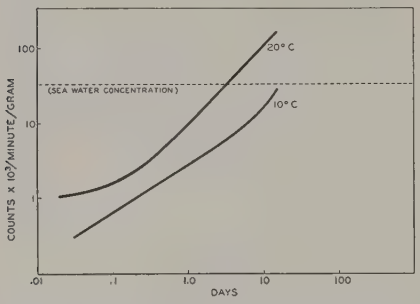

FIGURE 8. Uptake of Sr^{89} by Larval Flatfish.

that strontium was taken up more rapidly at the higher temperature. Thus at one day, the fish at the lower temperature had less than one third of the radioactivity of the fish at the higher temperature. The graph also shows that very young fish continue to take up strontium from solution very rapidly at 14 days, while at 14 days the *Tilapia* had reached an apparent steady state condition.

The uptake of $zinc^{65}$ by croakers was studied at the R.L.F.W.S. These fish were fed the isotope in hardened gelatine. After 12 hours only about 27 per cent of the dose remained in the fish (Table 8). The distribution of zinc is quite different from that of strontium. About 90 per cent of the strontium retained by the various fishes used at the H.M.L. was found in the gills, bones, and integument. Zinc, however, is concentrated mainly in the liver and spleen. The muscle and bone, because of their bulk accounted for a large part of the total $zinc^{65}$ of the body. The turnover times of the zinc-containing compounds of the skin, muscle and bone were slow, whereas those of the internal organs were relatively rapid.

The uptake of radiocesium by fish was studied at the R.L.F.W.S. Table 9 shows the distribution of $cesium^{137}$ which was fed to little tuna. It can be seen that the liver, heart, spleen, and kidney rapidly take up the cesium, but these organs also lose the cesium during the following week. Muscle, gonad, brain, and skin, on the other hand, continue to accumulate the cesium faster than they lose it.

TABLE 8 $Zinc^{65}$ DISTRIBUTION IN CROAKERS (*Micropogon undulatus*) 12 HOURS AFTER ORAL ADMINISTRATION

Tissue or Organ	Per cent of total weight	Weight in grams	$Zinc^{65}$ mμc/gm.	$Zinc^{65}$ mμc per tissue or organ	Per cent of total body $zinc^{65}$
Muscle	80	48.80	1.6	78.1	44.7
Bone	11	6.71	5.5	36.9	21.1
Gills	2	1.22	10.9	13.3	7.6
Liver	0.8	0.49	40.7	19.9	11.4
Gonads	0.4	0.24	17.6	4.2	2.4
Kidney	0.3	0.18	41.5	7.5	4.3
Heart	0.2	0.12	14.0	1.7	1.0
Spleen	0.1	0.06	25.3	1.5	0.9
Remainder ..	5.2	3.17	3.7[1]	11.7	6.7
Skin, scales					
G I tract		60.99		174.8	
Blood					
Brain					
Eyes					
etc.					

[1] Based on skin and scales

Dose per fish—6,100 mμc

Distribution after 12 hours

Tissues	3 percent
G I tract	24 percent
Loss	73 percent (mostly excreted)

The accumulation of cesium in solution was demonstrated by keeping croakers in Cs^{137} enriched sea water. The water was changed daily to maintain a relatively constant concentration. Figure 9 indicates that during the 29 days, the heart, spleen, liver, brain, and muscle continued to accumulate the cesium. The concentration factor for the heart, spleen, and liver, was about 10, but this value is far below an equilibrium value.

TABLE 9 THE DISTRIBUTION OF $CESIUM^{137}$ IN THE TISSUES OF THE LITTLE TUNA AS A FUNCTION OF TIME

	Cs^{137} content in μc/g. wet wt. Days after the dose			
Organ	1	3	6	8
Spleen	3.46	3.29	3.22	1.57
Liver	9.07	4.71	3.45	2.59
Kidney	3.13	2.58	1.78	0.95
Heart	6.17	3.15	2.52	1.57
Bone	0.41	0.40	0.17	0.26
Eye	0.30	0.26	0.31	0.30
Muscle	0.46	0.67	0.87	0.79
Gonad	0.54	0.70	1.33	1.34
Brain	0.30	0.35	0.69	0.66
Skin	0.29	0.46	0.41	1.01

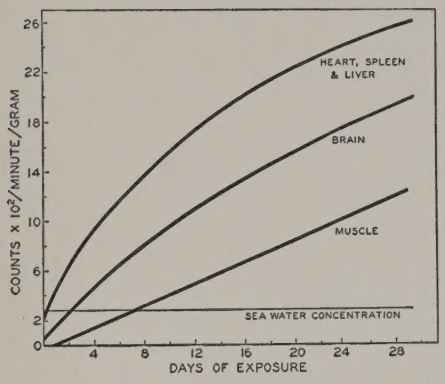

FIGURE 9. Accumulation of Cs^{137} by Croakers Kept in Sea Water Containing 5×10^{-8} Microcuries/Ml.

The relative concentration of cesium by the various organs is roughly the same for croakers, tuna, or bluefish. The same rank order among the organs is maintained both from ingestion, and from direct uptake.

Menhaden, a filter feeder, were put into sea water with ruthenium^{106} that had been co-precipitated with calcium carbonate. Although a considerable amount of particle settling occurred, the menhaden took up the ruthenium in the digestive tract, but the tissues of the fish did not become radioactive to an appreciable extent. Similar experiments using menhaden fed with Ru^{106} labelled *Arbacia* plutei, or Ru^{106} labelled *Nannochloris* cells, gave parallel results. In the latter experiment the fish were allowed to eat the labelled cells for four hours, and then they were put in running sea water. At the time of transfer about 92 per cent of the ingested dose was found in the digestive tract. The gills had 0.64 per cent of the dose, and the remainder of the fish, including the skin, had 0.76 per cent. At 128 hours, only 0.05 per cent of the ingested dose remained in the digestive tract. There was 0.25 per cent in the fish body or on the skin surface, and 0.01 per cent in or on the gills. At no time was there an appreciable increase in the radioactivity of the body of the fish.